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CONTENTS

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FLORAL HISTOGENESIS IN THE MONOCOTYLEDONS

I. THE GRAMINEAE

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[*Manuscript received October* 29, 1956]

Summary

The pattern of floral histogenesis in a representative species from each of six tribes of the Gramineae is shown to be similar to that described in a previous communication for *Triticum*.

Periclinal division of sub-hypodermal cells characterizes the origin of spikelet, flower, and stamen primordia. Periclinal divisions also occur in hypodermal cells during flower and stamen formation; and such divisions are more frequent at stamen initiation than at the initiation of flower primordia. Periclinal division of dermatogen cells never occurs during the formation of these organs, but is, on the other hand, a constant feature in the formation of glumes, lemma, palea, lodicules, and carpel. The hypodermis always contributes to the tissues of the glume and lemma primordia; it less frequently contributes to the tissues of the lodicule and palea, and only occasionally to that of the carpel.

The morphology of the gramineous flower is discussed on the basis of floral histogenesis and the pattern of provascular tissues in the gynaeceum.

I. INTRODUCTION

The literature dealing with floral histogenesis in angiosperms has been reviewed in a previous communication (Barnard 1955). It was stated that the few studies which had been made had concerned only dicotyledonous plants. The author has since become aware of a paper by Holt (1954) in which the histology of organogenesis of the flowers of *Phalaris arundinacea* L. and *Dactylis glomerata* L. was described. Holt (1955) has since published illustrations of floral histogenesis in *Avena*. The descriptions and interpretations of Holt differ from those of the author (Barnard 1955) dealing with floral histogenesis in *Triticum aestivum* L.

In the present paper, floral histogenesis is described for species in six other genera of the Gramineae in order to determine how far it varies amongst representative genera and how it compares with that described for *Triticum* on the one hand, and *Phalaris*, *Dactylis*, and *Avena* on the other.

The six species and the tribes to which they belong are:

Bambusa arundinacea Willd.	Bambuseae
Lolium multiflorum Lam.	Hordeae
Bromus unioloides Kunth. (*Bromus catharticus* Vahl in "Standardized Plant Names" (C.S.I.R.O. 1953))	Festuceae
Danthonia setacea R. Br.	Aveneae
Ehrharta erecta Lam.	Phalarideae
Stipa hyalina Ness.	Agrostideae

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Some observations on the early vascular development in the gynaeceum of the above species and in *T. aestivum* are also given. The conclusions drawn from these observations are complementary to those derived from the histogenetic studies.

The work here reported constitutes the first part of a project which aims at contributing to our understanding and interpretation of floral morphology through a study of the histology of organogenesis. Comparable studies are being made in other families of the monocotyledons.

II. Material and Methods

Material of *Bambusa arundinacea* was obtained from the Botanic Gardens at Brisbane, Qld. For the other species material was collected from naturally occurring plants at Canberra, A.C.T., or from plants cultivated there in pots.

Dissections of all materials were made, stained in acid fuchsin, and examined under the stereomicroscope. These examinations simplified interpretation of the sectioned material.

The usual procedures were used for embedding in paraffin wax and sectioning. Small objects were correctly orientated for cutting by gently melting the surrounding wax with a hot needle under the stereomicroscope, noting the disposition of the subject, and marking the desired plane of sectioning. Sections were cut at 7 μ. Various staining combinations were used, the most generally satisfactory being iron alum haematoxylin counterstained with erythrosin in a mixture of equal parts of alcohol and xylene.

Drawings were made by photographing the subject and tracing a projected image from the negative.

III. Bambusa arundinacea

Flowering in *B. arundinaceae* is periodic; Arber (1934) and Bews (1929) state that this species flowers at intervals of about 32 years. Whilst this is no doubt true for gregarious and major blossoming, sporadic flowering occurs at much shorter intervals. The spikelets are borne in condensed panicles, each spikelet consisting of two basal glumes and three to five distichously arranged florets. Each floret is subtended by a lemma, and a small sterile lemma often occurs just above the uppermost fully developed and fertile floret. Actually, from six to eight flower primordia are initiated upon the spikelet axis but the distal three fail to develop to maturity. The floret is typical of the Bambuseae and consists of palea, three lodicules, six stamens, and a unilocular gynaeceum containing a single ovule. The single style is divided into three long stigmatic branches.

The apex of the spikelet is made up of two outer single cell layers which together form a mantle over a central corpus (Fig. 4; Plate 1, Fig. 1). Cells of the outer layer (dermatogen) divide only by anticlinal walls except where a glume or lemma is initiated. Cells of the second layer (hypodermis) also divide only by anticlinal walls except where a lemma is initiated, though occasionally periclinal divisions also occur in this layer where a flower primordium is formed. Cells of both the dermatogen and hypodermis are usually rectangular and slightly elongated

in a radial direction. These characters and the regular disposition of the cells clearly delineate the two layers from the core. There is no evidence that either the dermatogen or hypodermis arise from apical cells and anticlinal cell divisions occur all over the dome-shaped apex. The corpus zone arises in a small group of merismatic cells at its apex; its cells are mostly polygonal and a single apical cell cannot be discerned. Cells in this zone rapidly become vacuolated and stain much less densely than those of the two outer layers.

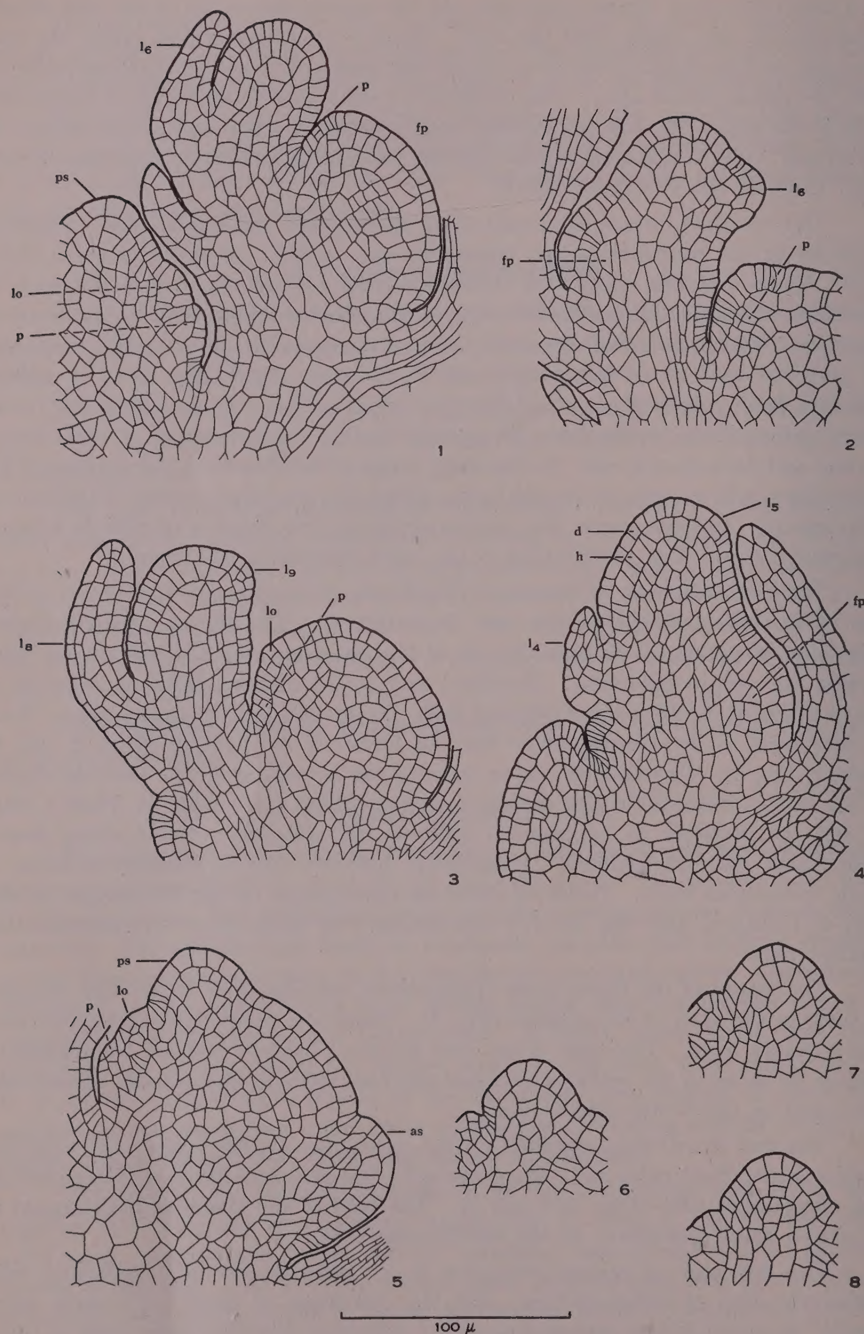
The lemma is formed from cells of the dermatogen and hypodermis; periclinal divisions in the hypodermis just below the apex initiate its differentiation (Figs. 2–4). These divisions occur in a transverse band around the axis of the apex in the area of lemma differentiation and involve three to four cells in the vertical direction. The periclinal divisions in the hypodermal cells are invariably followed by periclinal division of dermatogen cells in the same band (Figs. 2–4), though in this case fewer cells in the vertical direction are involved. The growth of the young lemma primordium results from the further division of derivatives of these hypodermal and dermatogen cells. In the early stages of development, derivatives of the dermatogen cells contribute largely to the apical and marginal growth of the lemma primordium. In later stages, the lemma grows by the division of cells in a basal merismatic area. The glumes arise in the same manner as the lemmas.

The first indication of the origin of a flower primordium is an increase in the size of hypodermal cells in the area of initiation. The flower primordia arise primarily, however, by division of cells of the outer layer of the core tissue (here termed the sub-hypodermis). Periclinal and semi-periclinal divisions occur in a group of about 12–16 sub-hypodermal cells. In longitudinal median section, three to four cells in the vertical plane may be observed so dividing (Figs. 2 and 4; Plate 1, Fig. 1). Occasionally one or more of the hypodermal cells near the centre of the young primordium also divides in the periclinal plane (Fig. 4; Plate 1, Fig. 1) and the divisions of hypodermal cells on the periphery of the young flower primordium may be inclined. Essentially, however, the hypodermis remains a single continuous layer. Periclinal divisions never occur in the dermatogen in the area of initiation and this layer is continuous over both flower primordium and spikelet axis.

The tissues of the young flower primordium are organized in the same manner as those of the apex of the spikelet (Fig. 1). There is a dermatogen, a hypodermis, and a central core. The cells of the core do not, however, become vacuolated as quickly as those in the spikelet axis and the core tissue is much more extensively developed in the flower primordium.

The first floral organ initiated on the primordium is the palea; the lodicules develop next. Both palea and lodicules arise by the periclinal division of hypodermal and dermatogen cells (Figs. 1–3 and 5). The bulk of the tissue of both organs is developed from derivatives of the dermatogen cells.

The first sign of stamen initiation is the enlargement of hypodermal cells within the area of differentiation; and the cytoplasm of these cells stains more readily than that of the surrounding cells. Periclinal divisions occur both in these cells and in cells of the sub-hypodermis (Figs. 5–8). Dermatogen cells in the area



[*For explanation of Figures 1-8, see opposite page.*]

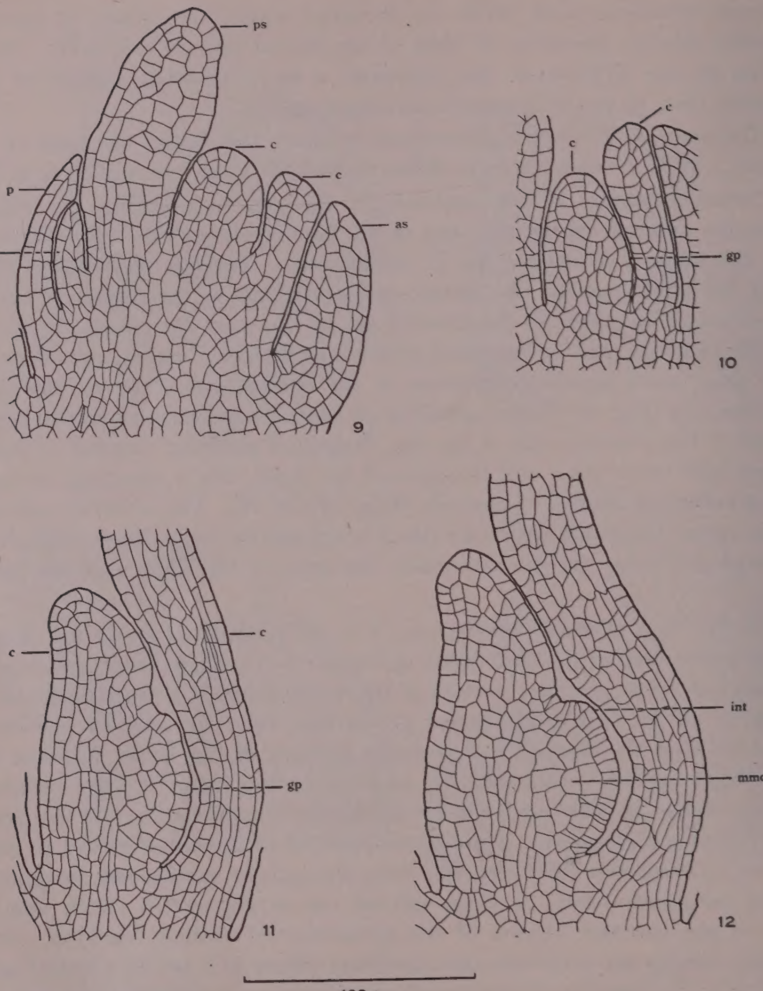
of stamen initiation never divide by periclinal walls. The mode of initiation is essentially similar, therefore, to that of the flower primordium itself. Periclinal divisions in the hypodermis are, however, a more constant feature of stamen formation than of flower primordia development.

The apex of the flower primordium is broad and flat at the time of stamen initiation; after the stamens have differentiated the apex becomes more elongated.

Carpel formation is first apparent in the periclinal division of dermatogen cells on the anterior side of the apex of the flower primordium. (See Figure 14 in which this stage is illustrated for *L. multiflorum.*) There is no evidence that the cells of the layer beneath the dermatogen contribute to the tissues of the carpel primordium. The carpel on the anterior side of the axis has grown into a definite foliar-like structure and by marginal growth has extended around the lateral flanks of the axis before periclinal divisions in the dermatogen occur on the posterior side of the axis (Fig. 9). These periclinal divisions occur at the tip of the floral axis and just to the posterior side of the tip. Repeated periclinal division of these dermatogen cells takes place and the apex of the floral axis is displaced so that it is directed anteriorly instead of upwards (Figs. 10 and 11). The posterior and anterior portions of the carpel are united by tissue which has its origin in periclinal divisions of dermatogen cells. In the meantime, the apex of the floral axis has increased in size.

On the basis of these observations, it is not possible to accept the usual view that the gynaeceum of the Gramineae is composed of a single carpel which encircles the floral axis. The posterior portion of the carpel arises at a morphologically more distal level on the axis of the flower primordium than the anterior portion. The relation between the anterior and posterior portions of the carpel is indeed similar to that between one lemma and the next succeeding lemma on the spikelet axis (see Figs. 3 and 4): the next succeeding foliar structure arises on the axis at a morphologically higher level. The posterior portion of the carpel should be regarded therefore, as a separate foliar structure from the anterior portion and the gynaeceum as being composed of two, or more, and not one carpel. Arber (1926, 1934), from studies of the vascular bundles of the gynaeceum of various bamboos, concludes that three carpels are involved—one anteriorly placed and two in a lateral position.

Figs. 1–8.—*Bambusa arundinacea*. Fig. 1.—A median longitudinal section of the apex of a spikelet showing a flower primordium (*fp*) in axil of the fifth lemma with the palea (*p*) arising. Early development of the palea (*p*) and the posterior lodicule (*lo*) is shown in the flower primordium in the axil of the fourth lemma. (*ps*)—the posterior stamen. Fig. 2.—Longitudinal section of apex of spikelet showing origin of the sixth lemma (l_6), a flower primordium (*fp*) in the axil of the fifth lemma, and the palea (*p*) in the next oldest flower primordium. Fig. 3.—Longitudinal section of apex of spikelet showing origin of the ninth lemma (l_9) and the palea (*p*) and posterior lodicule (*lo*) in the flower primordium in the axil of the seventh lemma. Fig. 4.—Longitudinal section of apex of spikelet showing origin of the fifth lemma (l_5) and a flower primordium (*fp*) in the axil of the third lemma. The dermatogen is indicated at (*d*) and hypodermis at (*h*). This section is shown in Plate 1, Figure 1. Fig. 5.—Longitudinal section through a flower primordium showing early development of the palea (*p*) and posterior lodicule (*lo*) and the initiation of the anterior stamen (*as*) and posterior stamen (*ps*). Figs. 6–8.—Represent successive longitudinal sections through the posterior stamen illustrated in Figure 5. Periclinal divisions in both hypodermis and sub-hypodermis are shown.



Figs. 9–12.—*Bambusa arundinacea.* Fig. 9.—A longitudinal section of a flower primordium showing *p*, palea; *lo*, the posterior lodicule; *ps*, the posterior stamen; *c*, the carpel; and *as*, the side of the anterior stamen. Divisions in the dermatogen on the posterior side of the floral apex indicate the origin of the posterior portion of the carpel. Fig. 10.—Shows the early development of the carpel and the almost apical position of the posterior portion of the carpel. The apex of the floral axis (*gp*) is now pointed in an anterior direction. Fig. 11.—Shows further development of the carpel and the reconstitution of the growing point (*gp*) of the floral axis. Fig. 12.—Shows the origin of the ovule from the growing point of the axis; the integument (*int*) is arising and the megaspore mother cell (*mmc*) differentiating.

This view is based primarily on the fact that three vascular bundles are seen in a transverse section of the ovary. One of these is situated in an anterior position and two in lateral positions and one bundle goes to each of the three styles. These

bundles are interpreted as the mid-veins of three foliar structures which have fused together. Arber (1934) further concludes that the ovule is borne on the fused margin of the two lateral carpels. The theory that only one carpel is involved interprets the anterior bundle as the midrib, and the lateral bundles as the marginal veins, of the single carpel.

Neither of these concepts seems very satisfactory and the matter is discussed further below. It may, however, be noted here that transverse sections through young gynaecia at successive levels show that the anterior provascular trace is the first to detach itself from the central core of provascular tissue in the floral axis. The traces which occupy the lateral positions detach at a higher level whilst the remaining sector of the provascular tissue in the axis continues directly to the ovule.

The apex of the floral axis develops into the ovule. The integuments arise by division of cells of the dermatogen in precisely the same way as the carpel arises (Fig. 12). A single hypodermal cell divides by a periclinal wall to give the megaspore mother cell and a parietal cell. The parietal cell divides again by periclinal and then anticlinal walls.

IV. Triticum aestivum

The floral histogenesis of this species has already been described (Barnard 1955). The following observations concern the development of the vascular tissue of its gynaeceum and in some measure assist us to interpret the nature of the gynaeceum of *Bambusa*. Serial transverse sections were made of florets of different ages but mainly from those showing differentiation of the megaspore mother cell and the megaspore.

Subsequent to the detachment of a vascular trace to each of the three stamens, the provascular tissue of the floral axis is arranged in the form of a cylinder (Fig. 13*A*; Plate 1, Fig. 3). At a slightly higher level, a provascular trace is detached from this central cylinder on the anterior side (Fig. 13*B*). This trace may consist of only a few elements, one of which is slightly lignified. It is rather discontinuous, being well differentiated at some levels and hardly discernible at others. A gap is left in the central provascular cylinder just above where it is detached. At almost the same level, or a little higher, a gap appears in the central provascular cylinder on its posterior side. There is, however, no sign of the detachment of a provascular strand on this side (Fig. 13*C*). Two lateral strands then become detached (Fig. 13*D*) and diverge into latero-posterior positions. The residue of the central provascular cylinder continues directly to the ovule (Fig. 13*E*). At the level of the ovule, the two lateral provascular traces and the anterior one are quite well developed (Plate 1, Fig. 4; Fig. 13*F*), but just above this level the anterior provascular trace disappears (Fig. 13*G*; Plate 2, Fig. 1). One of the lateral traces goes to each branch of the style (Fig. 13*H*). The top of the loculus is continued upwards as a stylar canal. Here marginal growth is very marked and derivatives of cells of dermatogen origin are disposed in radial series simulating cambial activity (Plate 2, Fig. 1).

There is occasionally a detachment of tissue from the posterior side of the style which forms a short stump or branch (Fig. 13*I*; Plate 2, Fig. 2). More frequently a short branch is formed also on the anterior side. The style then divides

into its two main branches and considerable marginal growth is evident on the inner face of each branch (Plate 2, Fig 3).

Towards the tip of the style, in the stigmatic region, there often appear in addition to the main provascular strand (Plate 2, Fig. 2) one or two other small groups of provascular-like cells. One of the groups is situated at each side of the stylar branch near its inner surface and the general structure of each branch of the style at this level is comparable to that of the tip of a young lemma. In Plate 2, Figure 4, a transverse section through the tip of a lemma is shown for comparison

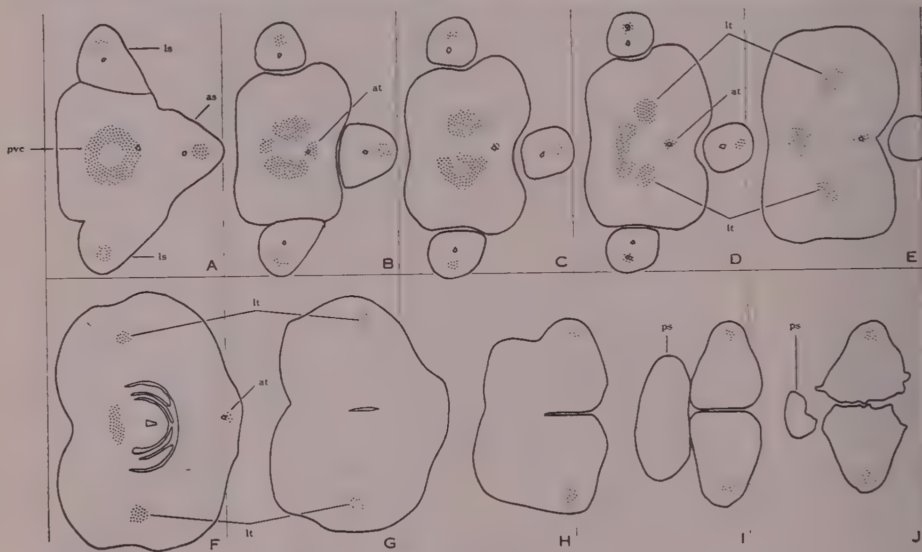


Fig. 13.—*Triticum aestivum*. A series of transverse sections from the base upwards of a young floret at the megaspore mother cell stage. *A*, below ovary level there is a cylindrical provascular cylinder (*pvc*) in the floral axis: *as* represents the anterior stamen bundle, and *ls* the lateral stamen bundles. *B*, detachment of the anterior carpellary trace (*at*) from the central provascular cylinder. *C*, divergence of the anterior carpellary trace and the presence of a posterior gap in the provascular cylinder. *D*, origin of the two lateral carpellary traces: and *E*, the divergence of these traces. *F*, at ovule level the three carpellary traces (*at* and *lt*) are developed. The residual of the provascular of the floral axis enters the ovule. *G*, above ovule level the anterior carpellary trace disappears. *H*, the beginning of the division of the style into two branches. *I*, the two stylar branches and a short posterior branch (*ps*). *J*, similar to *I* but at a higher level.

with the transverse sections of the stylar branches in Plate 2, Figure 2. In the section of the lemma tip, the marginal growth, as seen in the radial disposition of cells from its adaxial surface, is well marked. There are three groups of provascular tissue. The most highly developed group on the abaxial side represents the mid-vein of the lemma; the two small groups on the adaxial side represent the marginal veins.

From these observations it is reasonable to suggest that the gynaecum is composed of probably four foliar-like structures which are fused together. The morphologically lowest, or first, is the anterior unit, the second is the posterior unit,

and the two lateral units are the most distal. The reasons for postulating a posterior unit are: (1) the occurrence of a leaf gap in the provascular cylinder of the axis in that position which a trace to a posterior unit would subtend; (2) the occasional appearance of a short posterior stylar branch; and (3) the high level of the position of origin of the carpel on the posterior side of the floral axis as compared with the level of origin on the anterior side. The posterior unit has been reduced most and the two lateral units least. In *Bambusa*, the anterior unit is not so reduced as in *Triticum*, i.e. the third stylar branch in *Bambusa* is homologous with the anterior stump-like branch from the style of *Triticum*.

V. Lolium multiflorum

In *Lolium* the inflorescence is a spike and in the material of *L. multiflorum* examined there were five florets per spikelet. The florets are arranged on the rachilla in the same plane as that of the spikelets upon the axis. The terminal spikelet has two glumes but only one is developed in the lateral spikelets: the single glume in the lateral florets is the upper one.

The general developmental morphology of the inflorescence has been described for *Lolium perenne* L. by Evans and Grover (1940) and for *L. italicum* Braun, *L. perenne* L., and *L. multiflorum* Lam. by Cooper (1951).

For this species, the histology of the developing inflorescence was examined as well as the histogenesis of the spikelet and flower.

The tissues of the apex of the developing inflorescence are organized into a dermatogen, hypodermis, and core. The spikelet primordia originate by divisions in the sub-hypodermal layer. Inclined divisions occur in the hypodermal cells on the periphery of the area of initiation but no definite periclinal divisions were seen. No periclinal divisions occur in the dermatogen. Each spikelet primordium is subtended by a leaf or bract initial which arises by periclinal divisions in the dermatogen and hypodermis. The leaf initials towards the distal end of the spike progressively fail to develop and in the most distal ones are represented by the division of only a few cells. Histogenesis of the spike is, therefore, similar to that of *T. aestivum* (Barnard 1955) and *P. arundinacea* (Holt 1954). It might be noted here that whilst figures 7 and 8 in Holt's paper and his descriptions are correct, the heavy lines delineating the second tunica layer (i.e. hypodermis) seem inaccurately placed in his figure 5 in areas of branch initiation.

The histogenesis of the developing spikelets is also similar to *Triticum* except that the glumes and lemmas with the flower primordia they subtend are developed in the same plane as that of the spikelets upon the axis of the spike instead of in the plane at right angles. The periclinal divisions in the dermatogen and hypodermis initiating the upper glume and the first lemma on the lateral spikelets occur almost simultaneously and opposite each other in apparently the same transverse plane. It is exceedingly difficult to determine at this stage which is the morphologically lower on the spikelet primordium. The first lemma which is formed on the adaxial side of the primordium has its origin in the division of dermatogen and hypodermal cells only two or three cells distant from the junction of the primordium with the spike axis. There is no indication at all of the abortion of a glume initial below the

first lemma. The first lemma initial is in fact developed from that point on the primordium where one would expect the lower glume to arise. The two glumes

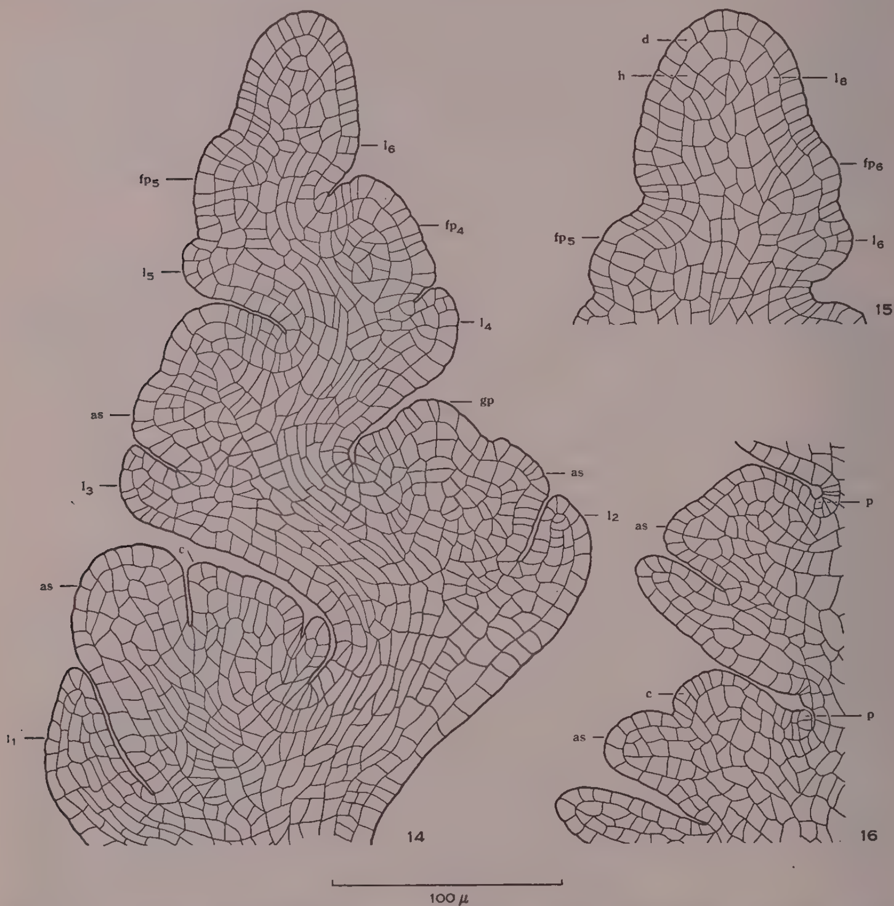


Fig. 14.—A median longitudinal section of a spikelet of *Lolium multiflorum* showing the origin of the lemma at l_6 and its progressive development in l_5–l_1; the origin of the flower primordium at fp_5 and its early development in fp_4; the origin of the palea and anterior stamen (*as*) in the flower primordia in the axils of the third and second lemmas; and the origin of the carpel in the most advanced flower primordium. Fig. 15.—A longitudunal section of the apex of the spikelet of *Danthonia setacea* in which the dermatogen (*d*) and hypodermis (*h*) are clearly shown, together with the origin of the lemma at l_8 and l_6, and the flower primordium at fp_6 and fp_5. Fig. 16.—Longitudinal section of two flower primordia of *Danthonia setacea* showing origin of the palea (*p*), the anterior stamen (*as*), and the carpel (*c*).

of the terminal spikelet with the succeeding lemma are formed in precisely the same fashion as in *Triticum*.

Six or seven flower primordia arise on the spikelet though only five develop to maturity. Histogenesis is illustrated in Figure 14, which represents a composite

drawing of two successive sections. The organization of the apex is similar to that described here for *Bambusa* and previously for *Triticum* (Barnard 1955). The lemmas arise by periclinal division of dermatogen and hypodermal cells; the flower primordia are initiated by division of both hypodermal and sub-hypodermal cells. The palea, lodicules, and carpel arise as described for *Bambusa*. The first indication of the initiation of stamens is the enlargement of hypodermal cells in the area of differentiation. Periclinal division in hypodermal cells and of sub-hypodermal cells follow. There is never any periclinal division of dermatogen cells in the initiation of the stamen.

The vascular anatomy of the young gynaeceum is similar to that described for *Triticum* except that above the point of detachment of the stamen traces the provascular tissue of the floral axis is in the form of a central core rather than a cylinder.

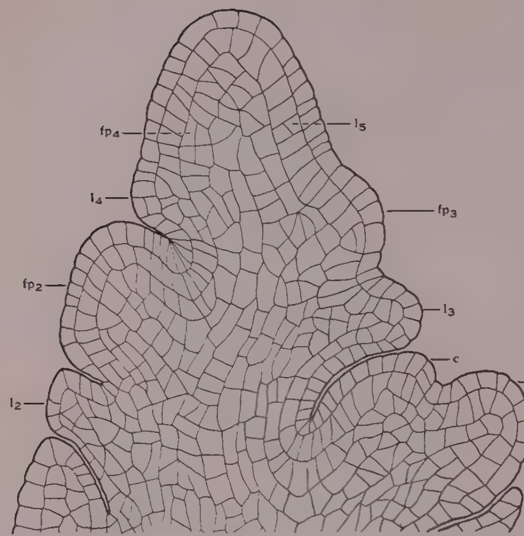
VI. Bromus unioloides Kunth. (Bromus catharticus Vahl in "Standardized Plant Names")

The spikelets of *B. unioloides* are borne in a panicle. Each spikelet has two glumes and each flower a palea, three stamens, two lodicules, and a unilocular ovary with bifid style. In the material examined of *B. unioloides*, six or seven flower primordia were differentiated but only five of these developed to mature florets.

The organization of the apex of the spikelet axis (Fig. 17) is similar to that described for *Bambusa* and *Lolium*. The lemma arises in the same manner as described for these species. The flower primordium arises by periclinal divisions of sub-hypodermal cells. Periclinal division of hypodermal cells is rare (Fig. 17) and then takes place at the centre of the area of origin (cf. *Triticum*). The initiation of the stamens is first evident in the enlargement of hypodermal cells: periclinal division of these hypodermal cells (Fig. 18) is accompanied by periclinal divisions in sub-hypodermal cells (Fig. 19) in the usual way. The outer of the two cells resulting from the periclinal division of a hypodermal cell does not appear to divide periclinally again and further divisions are only by anticlinal walls. The continuity of the hypodermis as a single layer of cells is thus re-established. The inner of the two cells on the other hand may divide again periclinally (Fig. 18).

Divisions in the dermatogen and hypodermis initiating the palea occur later than in the other species examined. The first divisions initiating the palea do not occur before differentiation of the anterior stamen and sometimes cannot be observed until after the carpel has been initiated.

The carpel arises by divisions of the dermatogen on the anterior side of the axis; periclinal division of dermatogen cells takes place later on the posterior side of the axis (Fig. 20). The divisions on the posterior side do not occur so near the tip of the floral axis as in *Bambusa* (cf. Fig. 9), nor indeed as in *Triticum* (cf. Barnard 1955). The archesporial cell which gives rise to the megaspore mother cell is differentiated very early and may be clearly discerned at the time when the divisions in the dermatogen initiate the carpel on the posterior side of the axis. The megaspore mother cell is formed before the carpel on the posterior side has made any appreciable growth and when the gynaeceum still appears open on this side.



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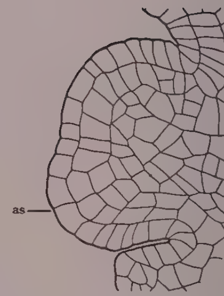

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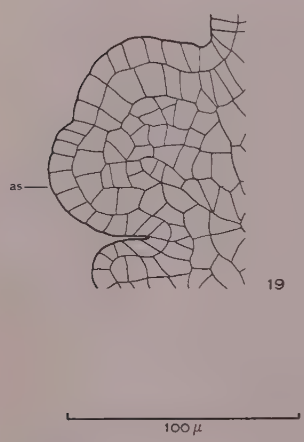

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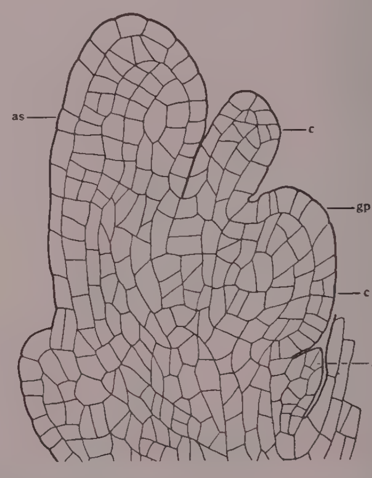

20

Figs. 17–20.—*Bromus unioloides.* Fig. 17.—A median longitudinal section of the apex of a spikelet. The origin and development of the lemma is illustrated at l_5-l_2; and of the flower primordium at fp_4–fp_2. On the oldest flower primordium the anterior stamen is developed at *as* and a division in the dermatogen initiates the carpel (*c*). Fig. 18.—A longitudinal section through a young flower primordium showing periclinal divisions in the hypodermis associated with the origin of the anterior stamen (*as*). Fig. 19.—A longitudinal section through a young flower primordium showing periclinal divisions in the corpus tissue associated with the origin of an anterior stamen (*as*). Fig. 20.—A longitudinal section of a flower primordium showing anterior stamen (*as*); carpel (*c*); growing point of the floral axis (*gp*); and palea (*p*). The periclinal division of two dermatogen cells represents the origin of the carpel on the posterior side of the axis.

Knobloch (1944) states that the gynaeceum of *Bromus inermis* Leyss is tricarpellate although he offers no evidence to support this conclusion. He also states that "The base of the ovary contains one large vascular bundle which continues up the high inner (posterior) carpel giving off first a branch to the ovule and then a branch to each style and terminating before the apex of the ovary is reached". This description is not true of *B. unioloides* where the vascular pattern is comparable to that described above for *Triticum*. Examination of florets which were at the megaspore mother cell to megaspore stage showed a single provascular trace above the level where traces to the stamens had become detached. This provascular bundle was in the form of a central core rather than as a cylinder as in *Triticum*. At a slightly higher level, this central core of provascular tissue became diffuse and the origin of the anterior and lateral traces could not be distinguished with certainty. Just below ovule level, however, an anterior trace and two lateral traces as well as a provascular trace to the ovule were developed. Both the anterior and lateral traces varied in their development and were discontinuous. The anterior trace disappeared at the top of the loculus whilst the lateral traces became more highly developed at this level and one continued up each stylar branch. Both posterior and anterior stylar stumps were sometimes developed.

VII. Danthonia setacea

In *D. setacea* spikelets of a paniculate inflorescence bear three or four florets. Two glumes are situated at the base of each spikelet and the flowers are normal. Some eight or nine flower primordia are differentiated upon the rachilla but only the basal three or four develop to maturity.

The organization of the spikelet apex and origin of the glumes and lemmas are as described for the previous species (Fig. 15, Plate 1, Fig. 2). The flower primordia arise by periclinal division of both hypodermal and sub-hypodermal cells (Plate 1, Fig. 2) and the stamens arise in similar fashion (Fig. 16). The palea is initiated by periclinal divisions in the dermatogen at about the same time as the anterior stamen has its origin. The carpel originates in the dermatogen (Fig. 16) in the usual fashion.

The vascular system of the gynaeceum at megaspore mother cell stage is comparable with that of the species already described but no anterior trace is developed. Above the point of attachment of the three stamen traces and below the ovary there is a central core of provascular tissue. From this central core two lateral carpellary traces detach whilst the residual provascular tissue continues to the ovule. At ovule level the two lateral traces are well developed and one trace goes to each stylar branch. At no level could any sign of an anterior carpellary trace be discerned.

VIII. Ehrharta erecta

In *E. erecta*, single-flowered spikelets are borne in loose panicles. In each spikelet there are two basal glumes and two sterile and one fertile lemma. The flower differs from those already described in having six stamens.

The apex of the spikelet is organized into a dermatogen, hypodermis, and core, but the tissue of the core is not so easily distinguished from that of the hypodermis as in *Triticum*, *Bambusa*, *Lolium*, and *Danthonia*. This is because the cells of the hypodermis do not present the same palisade-like appearance in longitudinal sections. The glumes, both sterile lemmas, and the flowering lemma arise in precisely the same fashion as in the species described above.

After the formation of the third lemma, the apex enlarges. Its shape changes from that of a pointed to a flattened dome, a change which results from a lateral increase in the extent of the core tissue. The dermatogen is distinct but the hypodermis is not well marked as a separate and continuous layer. Instead of the cells for the most part being rectangular in longitudinal section, they are polygonal.

The palea arises by periclinal divisions in the dermatogen and in cells immediately below the dermatogen. These divisions occur in the position where morphologically the next lemma would be expected to originate. The apex of the spikelet therefore appears to become transformed directly into the flower primordium. There is no evidence that the flower primordium originates in the axil of the third lemma leaving a residual apex which is aborted. A flower primordium also arises in the axil of the second lemma. It, however, aborts before it has differentiated any parts.

The six stamen primordia appear almost simultaneously in a circle around the dome of the flower primordium. Though later the stamens are arranged in two groups of three—an inner and an outer—there is no sign of arrangement into two whorls at their origin nor can any sequence of origin be discerned. Because of the difficulty in distinguishing with certainty between cells of the hypodermis and those immediately below it, the origin of the stamens in these terms cannot be stated. It is clear, however, that the stamens arise by periclinal divisions in cells below the dermatogen. These divisions seemed to be primarily in cells immediately below the dermatogen, i.e. in the hypodermis.

The carpel arises in periclinal divisions of the dermatogen in the usual way.

Transverse sections of the gynaeceum at the stage when the megaspore mother cell is differentiated show that below the level of the ovule an anterior provascular trace is developed. This trace is clear at ovule level where two lateral provascular traces appear. The anterior trace is not discernible at higher levels, but the lateral traces become more highly developed. One lateral trace goes to each branch of the style.

IX. Stipa hyalina

In this species, the spikelets, which are borne in a panicle, consist of single cleistogamous florets. Growth of the lemma is very rapid and obscures the flower primordium at a very early stage of development. The anterior stamen also develops early and its primordium is large as compared with those of the lateral stamens. The two lateral stamens form filaments and anthers but are small and abortive; only the anterior stamen produces pollen and is functional. The palea is late to arise. A lodicule is formed on either side of the anterior stamen and each is partially fused laterally at its base with the filament of the stamen.

The development of the inflorescence axis was observed in this species. The apex has the organization previously described. Each branch of the inflorescence is subtended by a leaf initial. Leaf initials subtending the upper branches of the panicle do not develop further than several cell divisions. These leaf or bract initials arise in the usual manner through periclinal divisions in the hypodermis followed by periclinal division of dermatogen cells. The branch primordia arise primarily by periclinal division of sub-hypodermal cells; periclinal divisions were observed in the hypodermis but it is not certain how common such divisions are.

The flower primordium apparently develops directly from the apex of the spikelet primordium as in *Ehrharta*.

The lodicules, palea, stamens, and carpel arise in apparently the same fashion as described for previous species but detailed studies were not made. The palea arises at about the same time as the anterior stamen.

The principal difference between the development of the flower primordium in *Stipa* as compared with the other species lies in the relative rate of growth of the floral parts. The lemma and the anterior stamen develop very rapidly, the palea is delayed in development.

An anterior and two lateral, carpellary provascular traces are developed. The anterior trace disappears just above ovule level; the two lateral traces continue into the branches of the style.

X. Discussion

There is very little difference in the histology of floral organogenesis in the species which have been examined. It is similar to that previously described for *Triticum* (Barnard 1955). These species represent a reasonable cross section of gramineous types.

The rudimentary leaves, which subtend the spikelets, the glumes and the lemma, all arise in the same fashion. Their mode of origin is similar to that of the foliage leaf as described by Rösler (1930) for *Triticum* and Sharman (1945) for *Agropyron*. Periclinal divisions in hypodermal cells are followed by similar divisions in dermatogen cells. Derivatives of both dermatogen and hypodermal cells contribute to the formation of these organs, the corpus zone making no contribution.

The palea arises by the division of hypodermal and dermatogen cells though in some species a periclinal division of hypodermal cells does not always take place. In all cases derivatives of the division of dermatogen cells contributed most of the tissue of the palea. The position with respect to the lodicules is not so clear but in all those species where their origin has been examined, periclinal divisions in the dermatogen have been involved.

The carpel is derived almost entirely, if not entirely, from the dermatogen. Cells in the layer below the dermatogen contribute little if anything to the carpel primordium. The integuments of the ovule also arise through the division of dermatogen cells.

In all these organs, the periclinal division of dermatogen cells at the time of their initiation is a constant feature. In the formation of the foliage leaf, the glumes,

and the lemma, divisions in the hypodermis also contribute largely to the tissue of the young organ. The contribution of the hypodermis to the tissues of the lodicules, palea, and carpel is less; and the bulk, if not all, of the tissues of the palea and carpel is derived from the dermatogen of the flower primordium. Apical and marginal extension during their early stages of development by divisions in the outermost layer of cells is a characteristic mode of growth of all these "foliar" organs.

On the other hand, in the formation of branch, spikelet, flower, and stamen primordia, periclinal divisions *never* occur in the dermatogen. Periclinal divisions *always* occur in the outer layers of the corpus and generally in the hypodermis.

Periclinal walls have not been observed to occur in the hypodermis during the formation of inflorescence branches or spikelet primordia. These structures arise in a manner similar to that described for the vegetative bud in *Agropyron* by *Sharman* (1945). Periclinal divisions in the outer corpus, or sub-hypodermal layer, initiate their formation and derivatives of these cells give rise to the whole corpus of the new organ. Anticlinal divisions continue in both dermatogen and hypodermis and these layers are also continuous with those of the axis upon which the new organ arises.

In the formation of flower primordia, periclinal divisions occur in the hypodermis as well as in the sub-hypodermis and the extent to which these divisions take place varies with different species. Barnard (1955) noted in *T. aestivum* an occasional periclinal division in hypodermal cells towards the centre of the flower initial. In *Bambusa*, periclinal division of hypodermal cells is also infrequent but in the other species examined such divisions almost always occur. The outer cell resulting from such a division becomes part of the hypodermis and the inner cell part of the corpus of the new organ. In all species, however, the periclinal division of sub-hypodermal cells is the major characteristic of the origin of flower primordia.

Barnard (1955) noted that the origin of the stamen in *T. aestivum* was comparable with that of the flower primordium and differed from it mainly in the more frequent periclinal division of hypodermal cells. In the other species examined above periclinal division of hypodermal cells was always involved in stamen initiation. It is clear that the contribution made to the tissues of the young stamen, through the division of hypodermal cells and of cells beneath the hypodermis in the flower primordium, varies in the different grasses.

It is characteristic of both flower and stamen initiation that hypodermal cells within the area of initiation become enlarged and stain more deeply than the surrounding cells. There is no such obvious enlargement nor change in staining quality of cell content associated with the initiation of the "foliar" structures.

Holt (1954, p. 612) summarizes his conclusions with respect to the floral histogenesis of both *Phalaris arundinacea* and *Dactylis glomerata* by saying: "Foliage leaves, lemmas, stamens and pistil are derived from both the tunica and the corpus. Initiation of these organs can be detected by periclinal divisions in the corpus. Glumes, palea and lodicules are derived exclusively from the tunica". (The tunica is the name given to the dermatogen and hypodermis.) However, the illustrations given by Holt do not support his conclusions that the mode of origin of the lemma

is different from that of the glumes. Both structures seem to be derived exclusively from the tunica. There is also no evidence in his illustrations that the corpus is involved in the initiation of the carpel. His description of the origin of the branch and spikelet primordia agrees with that given here although, as pointed out previously, the limits of "tunica" tissue seem to be inaccurately shown. The histogenesis of the origin of the flower primordium is not described but the illustrations show periclinal divisions in the cells of the corpus and of the hypodermis. With respect to *Avena*, Holt (1955) says that the lemma is initiated in the peripheral layer of the corpus, the stamen is leaf-like in its derivation and the carpel also is foliar in its ontogeny. His illustrations, however, are not inconsistent with the picture of the histogenesis of these organs which has been presented here.

It is, therefore, concluded that the pattern of floral histogenesis previously described for *T. aestivum* (Barnard 1955) occurs generally throughout the Gramineae. The view that the floral structures on the basis of their mode of origin may be classified as cauline or foliar appears substantiated. Inflorescence branches, spikelets, flower primordia, and stamens belong to the cauline group; glumes, lemmas, palea, lodicules, and carpel to the foliar group.

The interpretation of the gynaeceum previously presented needs, however, to be modified. It is now suggested that the gynaeceum may be composed of three, and possibly four, fused foliar structures. There is a little evidence for postulating a posterior carpel which is very reduced in development. The origin of the posterior portion of the carpel at a morphologically higher level on the floral axis than the anterior portion suggests a separate structure. It is significant that in those species, particularly *Bambusa*, which are universally regarded as more "primitive" types, the difference in the morphological level at which the posterior portion of the carpel arises is most marked. Further evidence might be found to support this hypothesis by detailed study of other types of the Bambuseae.

There is more evidence suggesting that an anterior and two lateral units are fused to form the main body of the gynaeceum. The anterior unit is the morphologically lowest of the three and in all types except *Bambusa* the least well developed. It is to be regarded as morphologically lower than the lateral units because: (i) the anterior vascular trace joins the vascular tissue of the floral axis below the point of junction of the lateral traces, and (ii) divisions in the dermatogen initiating carpel development occur first on the anterior side of the floral axis. In the "primitive" *Bambusa*, the anterior unit is as well developed as the lateral units and each terminates in a stylar branch. In the other species, *Danthonia* excepted, an anterior carpellary provascular trace is developed to a varying degree but not to the same extent as the lateral traces. In *Danthonia*, no anterior trace was observed.

There also seems little doubt that the short stump-like anterior stylar branch often observed in *Triticum* and other species is to be interpretated as the homologué of the third stylar branch present in *Bambusa*. In like manner, the short posterior stylar branch observed in *Triticum* may be regarded as a vestigial fourth stylar branch from the postulated posterior carpel.

Arber (1929) has described the occurrence of six vascular traces and five or six and occasionally more stylar branches in the gynaeceum of *Bambusa nana*

Roxb. and species of *Ochlandra*. The posterior traces are not so well developed as those placed in the anterior and lateral positions. This suggests that more than four carpellary units were involved in the gynaecia of the prototypes of the gramineous flower.

The ovule apparently terminates the floral axis but this terminal position may be derived from an axillary position, i.e. the ovule might be regarded as being originally subtended by the fourth or posterior carpel, the apex of the floral axis by evolutionary reduction having become completely aborted. A parallel type of reduction is accepted in the generally recognized concept of the evolutionary development of the spikelet in the Gramineae. The single- and few-flowered spikelets are regarded as having been derived from many-flowered types by reduction of the distal and basal portions of the spikelets (Bews 1929). Reduction from the distal end of the spikelet has been the main evolutionary trend. This trend, in its ultimate expression, has resulted in single-flowered spikelets such as those of *Ehrharta* and *Stipa* in which, as we have observed, the flower primordium develops directly from the apex of the spikelet. There is no evidence in early ontogenetic development or histogenesis that the apparently terminal floret has been derived from a lateral position subtended by the lemma on the spikelet axis.

Accepted opinion is that the ovule has been derived from a carpel-borne position—whether one or three carpels are postulated. This opinion is based on the assumption that the gramineous gynaeceum is reduced or derived from the more "typical" monocotyledonous gynaeceum. This may or may not be correct. In like manner, the hypothesis that three carpels comprise the gynaeceum is "nice" because it makes the arrangement of parts trimerous. There is, however, no evidence in early ontogenetic development, nor in vascular structure, that the terminal ovule in the Gramineae has been derived from a carpel-borne position. The statement of Blaser (1941) that the eccentric, basal position of the ovule in the ovary of the Gramineae indicates an original parietal placentation seems to be quite speculative. With equal justification, an original axillary position of the ovule may be postulated.

Under this concept the posterior carpel originally subtended the ovule which was an axillary cauline structure. The lower lateral and anterior units represent carpels which during the course of evolution have become sterile and fused, assuming a protective function to the fertile carpel. Again, such a postulated evolutionary development would parallel the accepted view of the evolutionary development of the spikelet. In the development of the single- and few-flowered type of spikelet the lower and sterile glumes have increasingly assumed a protective function (Bews 1929). Arber's hypothesis that the gynaeceum is composed of three fused carpels also, of course, involves the concept of a sterile carpel.

It is, therefore, suggested that the flower in the Gramineae may be regarded as a branch system. The lemma is a bract which subtends this branch system; the palea and lodicules are foliar structures upon its main axis; the stamens represent reduced lateral branches bearing microsporangia; the gynaeceum is composed of fused foliar structures upon the distal portion of the main axis and the ovule is the ultimate reduction of a lateral branch bearing a megasporangium.

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Explanation of Plates 1 and 2

Plate 1

Fig. 1.—A median longitudinal section of the apex of a spikelet of *Bambusa arundinacea*. The dermatogen (*d*), hypodermis (*h*), and core tissues are shown. A young flower primordium is present in the axil of the third lemma. The origin of the fifth lemma is shown in the periclinal division of two dermatogen cells and underlying hypodermal cells, just to the right of the tip of the apex. ×390.

Fig. 2.—A median longitudinal section of the apex of a spikelet of *Danthonia setacea*. The origin of the ninth lemma is seen in the periclinal division of a hypodermal cell (l_9). Young flower primordia are situated at fp_7, fp_6, and fp_5. ×340.

Fig. 3.—A transverse section of the floral axis of *Triticum aestivum* above the separation of the stamens (*ls* and *as*) showing the provascular cylinder (*pvc*). ×140.

Fig. 4.—A transverse section through the ovary of *Triticum aestivum* at the megaspore mother cell (*mmc*) stage showing the two lateral carpellary traces (*lt*) and the anterior carpellary trace (*at*). ×140.

Plate 2

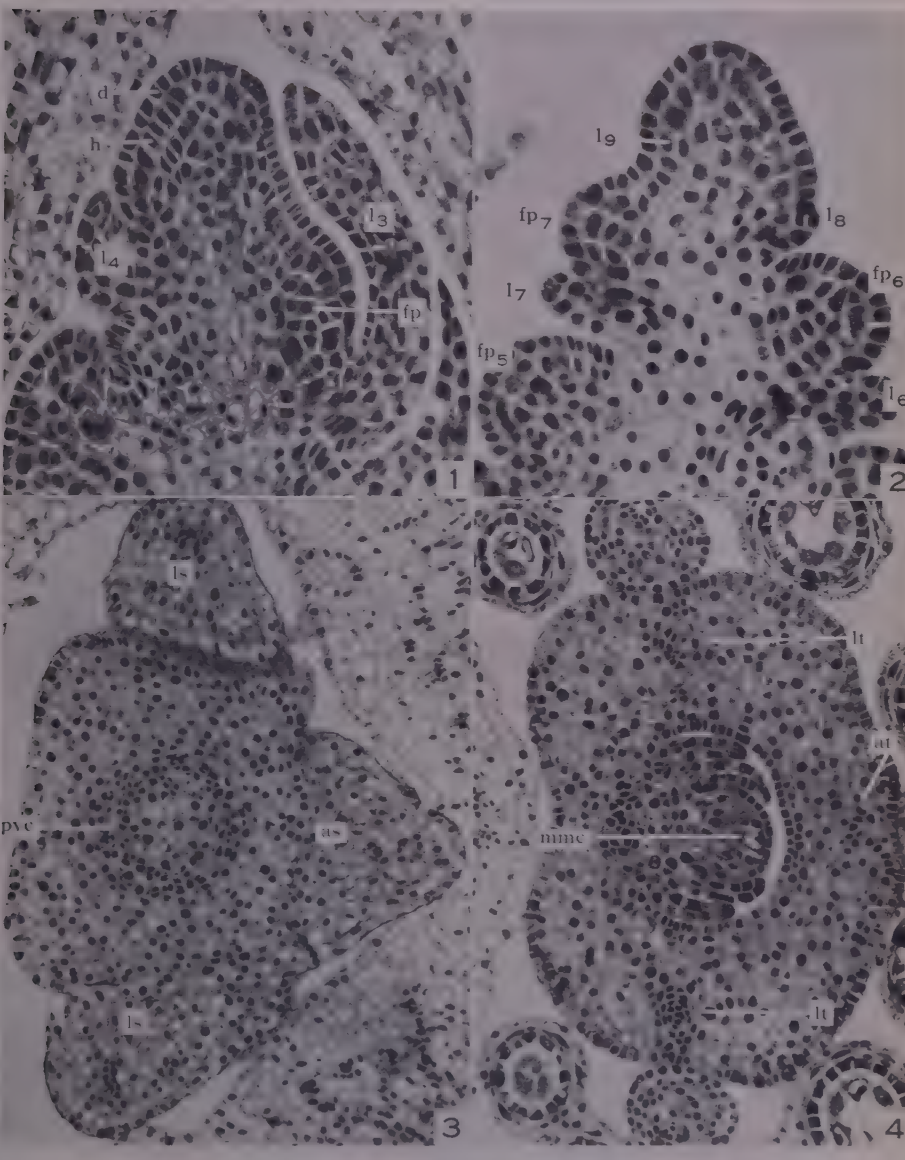
Fig. 1.—A transverse section through the top of the loculus of the ovary of *Triticum aestivum* at the megaspore mother cell stage. The lateral carpellary traces are at *lt*: the anterior trace has disappeared. Marginal growth from the face of the loculus is apparent. ×145.

Fig. 2.—A transverse section through the gynaeceum of *Triticum aestivum* just above the level where the two stylar branches diverge. At *ps* a posterior stylar branch is shown and at *lt* the lateral carpellary vascular trace. ×155.

Fig. 3.—A transverse section through the styles of a gynaeceum of *Triticum aestivum* at pre-megaspore mother cell stage showing the marginal habit of growth. The vascular trace in each stylar branch is discernible. $\times 360$.

Fig. 4.—A transverse section through the tip of a young lemma of *Triticum aestivum* for comparison with the transverse section of one of the stylar branches shown in Figure 2. $\times 270$.

FLORAL HISTOGENESIS IN THE MONOCOTYLEDONS. I



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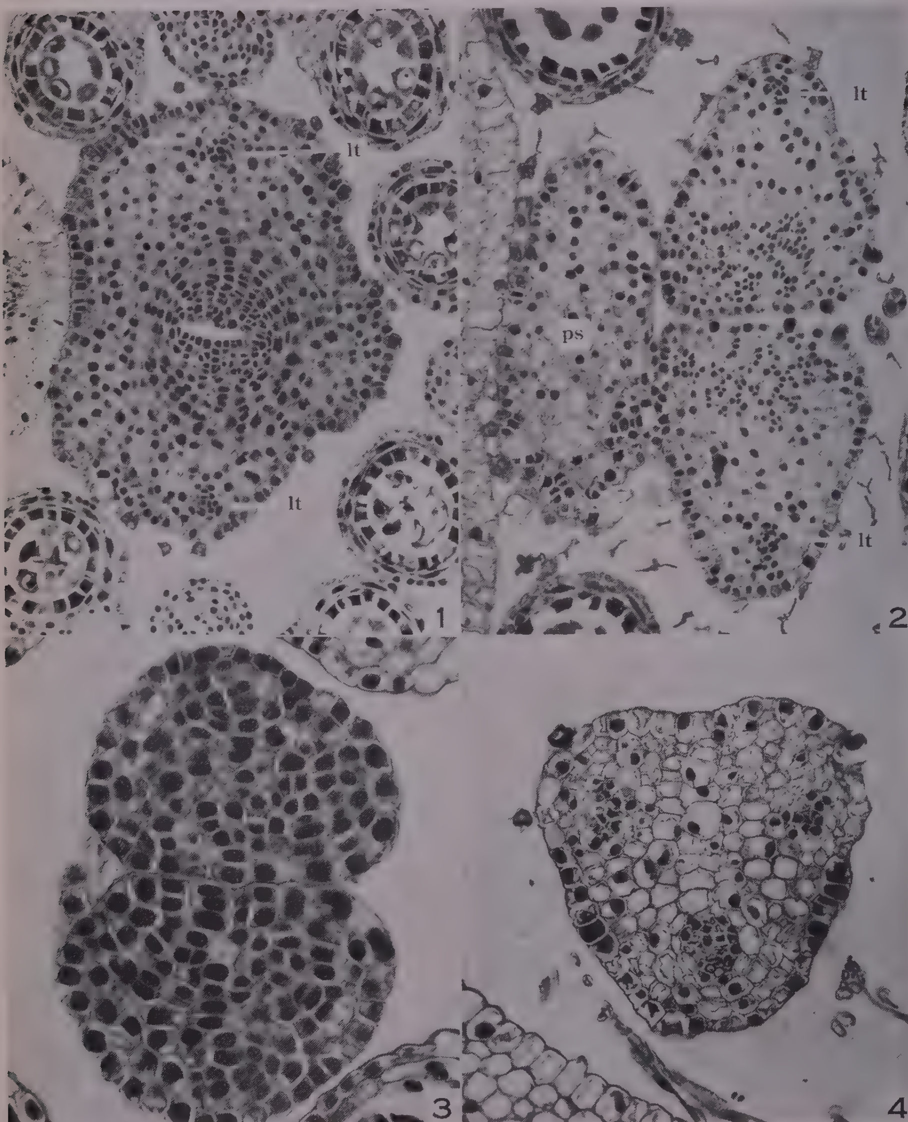

EUTYPA ARMENIACAE HANSF. & CARTER, SP. NOV., AN AIRBORNE VASCULAR PATHOGEN OF *PRUNUS ARMENIACA* L. IN SOUTHERN AUSTRALIA

By M. V. CARTER*

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Summary

A newly described Ascomycete, *Eutypa armeniacae* Hansf. & Carter, is shown to give the symptoms associated with "gummosis" disease of *Prunus armeniaca* L. (common apricot) in southern Australia.

Experimental evidence is produced to substantiate the hypothesis that *E. armeniacae* is the ascigerous stage of an imperfect *Cytosporina* sp. which has long been recognized as the causal organism of "gummosis", and that airborne ascospores of *E. armeniacae* are the only source of inoculum.

Ascospores of this species are shown to be well suited to aerial dissemination over long distances.

I. INTRODUCTION

The symptoms and significance of the disease of *Prunus armeniaca* L. (common apricot) known commonly as "gummosis" or "dieback" have been described in detail by Adam (1938) and Adam, Grace, and Flentje (1952). Since the isolation of the causal fungus, which was assigned tentatively by Samuel (1933) to the form genus *Cytosporina*, and the proof of its pathogenicity by Adam (1938), there has been much speculation concerning the mechanism of transmission of the disease in the field, and significant developments have been as follows.

Adam (1938) showed that wounds which exposed the wood were necessary before infection could take place. Transmission by the pruning saw was demonstrated experimentally in 32 per cent. of test cuts made during two seasons, but transmission did not occur in a proportion of these which were left uncovered after the cut was made.

Grace (unpublished data 1949) found that infections occurred apparently at random in relation to districts and to individual orchards, and, on any one tree, separate infections seldom or never occurred in a manner suggesting spread from one limb to another. The infection rate generally was highest in non-irrigated districts.

White (1945) obtained *Cytosporina* cultures from agar plates exposed after rain in Tasmanian apricot orchards. These cultures were shown by the present author in 1955 to be pathogenic; their origin was clearly airborne inoculum.

Carter (1955) isolated a species of *Eutypa* from dead apricot wood collected from apricot orchards in South Australia, Tasmania, and Victoria, and showed by inoculation that its pathogenicity was identical with that of *Cytosporina* isolates.

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Hansford has described this species of *Eutypa* as *E. armeniacae* Hansf. & Carter, sp. nov., and it is believed to be the first record of a pathogen in the genus *Eutypa*.

The hypothesis is here advanced that *E. armeniacae* and *Cytosporina* sp. are the perfect and imperfect stages respectively in the life-cycle of a single organism responsible for "gummosis" disease, and that airborne ascospores of *E. armeniacae* constitute inoculum by which the disease spreads, both within and between orchards.

II. Description of Eutypa armeniacae Hansf. & Carter, sp. nov.*

On the infected wood it first forms the conidial stage, *Cytosporina*:

Pycnidia scattered or gregarious, immersed in or almost superficial on an erumpent stroma, which is irregularly pulvinate, black in nature, rugulose with the pycnidia, to 2 mm dia.; in culture on apricot twigs this stroma is covered by a thin layer of loose hyaline hyphae with many erect ends, giving a greyish brown pruinose surface. The pycnidia are single or closely aggregate on the stroma, black, subglobose with apical round pore, or when immersed with a very short ostiole opening through the bark, separate or more or less confluent, or even sometimes compound with irregular loculi partially divided by intrusions or folds of the wall. Wall of superficial pycnidia 15–30 μ thick, the outer layers of interwoven dark brown stroma hyphae, the inner layers hyaline, of fine (1 μ thick) hyphae passing into the dense palisade of conidiophores lining the whole loculus. Conidiophores hyaline, simple, straight or slightly bent, 8–15 by 1 μ, forming single apical conidia. Conidia very numerous, hyaline, bent to arcuate, filiform, slightly attenuate to the obtuse ends, 18–25 by 1 μ, extruding from the apex of the pycnidium in yellowish tendrils, or when very moist forming a shining mass.

The perithecia develop only on branches estimated to have been dead from the disease for 4–5 years, after the conidial stage has more or less disappeared. While the covering bark is still intact on these branches, a thin black stroma gradually develops in the outer 4–10 layers of the underlying wood, filling these cells with

* **Eutypa armeniacae** Hansf. & Carter, sp. nov.

Stromata in lingo efformata, sub cortice secedenti, atra, late effusa, haud destincte marginata, rugulosa ob ostiolis peritheciorum, tenues; cellulae externae ligni plus minusve hyphis et pseudoparenchymati suffultae et superficie hyphis plurimis, intertextis, atrobrunneis, septatis, tortuosis, 4–9 μ cr. tectae. Perithecia in ligno immersa, monosticha, dense dispersa vel aggregata, distincta, ampulliformia, atra; collo usque ad 300 μ long. et ad 100 μ dia., prominulo (usque ad 160 μ alt.), apice obtuse rotundato, levi, haud sulcato, nigro, poro rotundato, breve periphysato, usque ad 35 μ dia. pertuso; corpus perithecii in ligno immersus, subglobosus vel lateraliter compressus, usque ad 450 μ dia. et alt.; paries perithecii submembranaceus, usque ad 30 μ cr., pluristratosus, pseudoparenchymaticus, cellulis externis crasse tunicatis, angulosis, atrobrunneis, illis internis diluotioribus, tenuiter tunicatis, compressibus. Asci cylindracao-clavati, numerosissimi, apice rotundati, deorsum in stipitem 20×1 μ attenuati, tenuiter tunicati, 8-spori, p. sp. circa 30×4 μ. Sporae 1–2-seriatae, imbricatae, allantoideae utrinque obtuse rotundatae, non vel lenissime attenuatae, curvulae, flavo-brunneolae, leves, continuae, $7\text{–}11 \times 1 \cdot 5\text{–}2$ μ. Paraphyses filiformes, simplices, hyalinae, continuae, mox plus minusve mucosae, 1 μ cr.

Hab. in ramis emortuis *Pruni armeniacae*, South Australia, WARI 4987 (typus), 7351–7363, etc.

dark brown hyphae and pseudoparenchyma, while on the surface of the wood, even after the bark has flaked away, there is a thin layer of much interwoven, tortuous, dark brown hyphae 4–9 μ wide. At full maturity the stroma is completely exposed as a thin, dull black layer, with indefinite margin, and with the rather closely scattered, slightly protruding (to 160 μ) necks of the underlying perithecia giving a slightly rough surface. Perithecia in a single layer, immersed in the wood below the stroma, with only the cylindric necks reaching the surface, closely scattered or aggregate, more or less globose below or laterally flattened from crowding; body of perithecium to 450 μ dia., with a fleshy-membranaceous wall up to 30 μ thick, consisting of several layers of dark brown, thick-walled pseudoparenchyma enclosing an intermediate layer of paler brown cells with thinner walls, which passes into the innermost layer 10–15 μ thick of hyaline, fibrous, much compressed tissue, continuous internally with the very numerous paraphyses below and the short periphyses lining the cylindric ostiole. The paraphyses are later obscured by the very numerous asci, which are formed over the lower two-thirds of the loculus surface. Asci cylindric-clavulate, attenuate below into a stipe about 20 by 1 μ, rounded at the apex, thin-walled, 8-spored, p. sp. about 30 by 4 μ. Spores 1–2-seriate and overlapping, allantoid, becoming pale yellowish brown when fully mature, slightly bent with obtuse, or sometimes very slightly attenuate, rounded ends, continuous, smooth, 7–11 by 1·5–2 μ, discharged from the asci as a solid mass of spores.

III. Experimental Tests of the Validity of the Hypothesis

Adam (1938) has shown that *Cytosporina* sp. satisfies the requirements of Koch's postulates in relation to "gummosis" disease.

If, then, *E. armeniacae* and *Cytosporina* sp. are stages in the life-cycle of the same organism, experimental proof is required that the following conditions obtain, namely:

(1) Both organisms produce identical disease symptoms.

(2) Both organisms have identical cultural characteristics and an inoculum of either one can, under appropriate conditions, give rise to all known spore forms of each.

The experimental procedure and results obtained in testing the various aspects of the hypothesis are presented under (*a*)–(*e*) below.

(*a*) *Pathogenicity Tests*

(i) *Single-ascospore Cultures*.—In isolating and testing single-ascospore cultures from each collection of perithecial specimens, the procedure was as follows.

A small piece of perithecial stroma was cut from the specimen, flamed lightly, and immersed in 2–3 ml of sterile distilled water in a Syracuse dish. In some cases it was necessary to crush the perithecia, but usually ascospores were discharged in abundance as soon as the material became thoroughly saturated. A loopful of the spore suspension was then spread evenly on the surface of 2 per cent. distilled water agar in a 9 cm petri plate and incubated at 25°C overnight. Usually 16–20 hr was sufficient to allow germination of a high proportion of the spores on the plate, and

the following day single germinated ascospores were transferred to marked positions on plates of potato dextrose agar containing $0 \cdot 1$ per cent. of "Marmite", this medium being suitable for rapid growth of *Cytosporina* sp. Incubation was continued until colonies 1–2 cm in diameter had developed; subcultures were then made from uncontaminated colonies to separate plates of the same medium.

Inoculations were made on young unpruned apricot trees at the Urrbrae Agricultural High School orchard, Fullarton, using a modification of the method developed by Adam (1938). Wood $\frac{1}{2}$–$\frac{3}{4}$ in. in diameter was used and, after inoculation, the wounds were covered with tinfoil and surgical bandage. Using known pathogenic cultures of *Cytosporina*, this method has never failed to give positive results, regardless of the time of year when inoculations were made. Pathogenicity tests were made in triplicate with each of three single-ascospore cultures from each specimen. In all, pathogenic single-ascospore cultures were isolated from 20 different collections representing 15 localities in South Australia, 1 in Tasmania and 1 in Victoria. Inoculations with these cultures all gave positive results in 2–3 months, the symptoms being indistinguishable from those resulting from *Cytosporina* inoculations in the same or comparable intervals of time. In some cases, the fungus was reisolated and reinoculated to fresh limbs; results of these tests were always in accordance with Koch's postulates.

(ii) *Ungerminated Ascospores*.—If *E. armeniacae* ascospores are the natural inoculum instrumental in spreading the disease, then natural infections must result from ascospores germinating on and penetrating suitable infection courts. It was therefore considered necessary to confirm this aspect of the hypothesis under controlled conditions.

Initial attempts failed presumably because of inadequate moisture for germination, but infections have resulted from the application of freshly prepared suspensions of ascospores to wounds of up to 28 days of age when inoculation was followed immediately by an incubation of 18–24 hr in a water-saturated atmosphere or by keeping the wounds moist for 3–7 days by means of saturated cotton-wool wicks. (See Plate 1, Figs. 1 and 2.)

It is noteworthy that failures have also resulted from inoculations incubated under moisture conditions which, at other times, have produced infections. Thus inoculations made in March 1955 and in January 1956 failed, whereas those made between May and October 1955 under comparable conditions were mostly successful. It is impossible to account for these differences until further series of inoculations have been made strictly under uniform incubation conditions, but the possibility of variation in susceptibility of the host during the growing season should not be overlooked.

(iii) *Conclusions*.—Results of pathogenicity tests on healthy apricot seedlings have demonstrated the ability of both mycelium and ascospores of *E. armeniacae* to penetrate the wood and set up "gummosis" infections indistinguishable from those which result from mycelial inoculations with *Cytosporina*. Condition (1) of the hypothesis is thereby fulfilled.

(*b*) *Cultural Characteristics and Spore Forms*

Comparison of a range of single-ascospore cultures of *E. armeniacae* with a range of *Cytosporina* isolates from "gummosis"-infected apricot limbs, grown on identical media, has revealed no apparent morphological differences in excess of those occurring between cultures within each group. Both groups have produced pycnospores with comparable morphology.

Repeated attempts have failed to secure perithecial development in the laboratory from either single or mixed isolates of *Cytosporina* sp. Substrates used have included a variety of laboratory agar media, various agar media supplemented by additions of apricot stem and leaf decoctions, and both living and dead apricot wood. Some of the wood cultures have been maintained for up to 3 years without any development of perithecia although pycnidia and pycnospore tendrils have been produced in abundance. Single and mixed ascospore cultures of *E. armeniacae* on sterilized apricot wood taken from limbs bearing perithecial stroma have also failed to reproduce perithecia in a period of 15 months. It is thought that fructification may require longer periods of time and the cultures are being maintained with this object in mind, but there is also a possibility that the conditions prevailing in these laboratory cultures may not meet the exacting requirements for fructification which are supplied by natural weathering of infected apricot limbs after their death.

Periodical inspections have been made of limbs inoculated in the field by the author since February 1953 but none of these has yet developed a perithecial stroma although many (including limbs inoculated with mixtures of several *Cytosporina* isolates) have been dead for over 2 years. The only supporting evidence comes from a series of limbs inoculated by Grace (unpublished data) in June 1949; several of these were developing stromatic tissue near the site of inoculation during 1955, and in January 1956 mature perithecia were found on one and immature perithecia on two others. Single ascospores isolated from this material yielded cultures of *E. armeniacae* whose pathogenicity was confirmed subsequently by inoculation.

The evidence from the 1949 inoculations is open to criticism on the grounds that infection by *E. armeniacae* ascospores may have taken place subsequent to the original *Cytosporina* inoculations; otherwise, all evidence from comparison of cultural characteristics and pycnospore morphology supports the hypothesis.

(*c*) *Distribution of* E. armeniacae *Fructifications in Relation to that of the Disease*

Perithecia of *E. armeniacae* have been found only on apricot wood which has been dead sufficiently long for the bark to be partially or completely sloughed off. It is possible that the developing stroma aids the latter process and hence that perithecial specimens appear older than uninfected wood of a comparable age. From field observations of naturally infected wood and of limbs inoculated by Grace in 1949 (see Section III(*b*)) the author believes that a period of at least 5 years must elapse following death of the infected host tissue before the perithecia develop. Perithecia occur on dead limbs still attached to the tree as well as on detached wood, but in the former case they are only found on trees which have been neglected for a number of years.

The distribution of *E. armeniacae* perithecia coincides with that of "gummosis" disease in South Australia, Tasmania, and south-western Victoria, and the proportion of infected trees in any locality appears directly related to the amount of perithecial fructification in the vicinity. Observations of the variation in disease incidence and production of perithecia between districts in South Australia whose mean annual rainfall differs greatly have shown that, where the mean exceeds 13 in., perithecia occur in abundance and disease incidence is high (50–84 per cent. of trees infected according to Grace's (unpublished data) 1949 survey); in irrigated districts whose mean is below 11 in., perithecia are exceedingly rare and disease incidence is much lower (18 per cent. of trees infected in the upper Murray irrigation districts in South Australia, according to Grace). During an intensive search for *E. armeniacae* perithecia in the latter districts in 1955, the author succeeded in finding only two occurrences, each of which was confined to a small zone of dead wood a few inches above soil level on a partly dead tree. It seems probable that the shelter of weed growth around the tree butt and moisture from irrigation water in such cases have supplemented the natural rainfall sufficiently to create a micro-environment suitable for fructification of the fungus in an environment which is otherwise unfavourable. The low natural rainfall (9–11 in. per annum) of these irrigated districts is evidently not sufficient *per se* to allow fructification, as perithecia were not found on dead wood in any of the numerous dumps on non-irrigated land in these districts. Similar dumps in higher-rainfall districts almost invariably contained fructifications of *E. armeniacae.*

(*d*) *Dissemination of* E. armeniacae *by Ascospores*

(i) *Requirements for Ascospore Discharge.*—Mature perithecia of *E. armeniacae* only occur on dead apricot wood in zones from which the bark has sloughed away; hence they are exposed to rapid wetting whenever rain falls. In laboratory tests, perithecia discharge free ascospores usually within 5–10 min when immersed in water. Spore counts made at intervals after immersion of a piece of perithecial stroma approximately 1 sq. cm. in surface area are given in Table 1.

When perithecia are immersed in water until discharge commences and then removed, spores are ejected forcibly as soon as the water film has receded from the ostioles and discharge may continue for 2 hr or longer, depending on the temperature and moisture content of the surrounding atmosphere. Discharge occurs as readily at 10°C as it does at room temperatures of 20–35°C, and spore counts of the order of 9×10^8 have been recorded following a single wetting of a 1 cm square specimen. A single specimen, wetted on nine different occasions which were separated by dry intervals varying from a few hours to over a month, has discharged spores abundantly after each wetting. It is likely that spore production within the perithecia continues, under suitable conditions, for many months and possibly for several years, but, as there is no way of assessing the amount of discharge which has occurred before the specimens are brought into the laboratory, their full potential spore production cannot be determined.

(ii) *Nature of the Unit of Dispersal.*—Ejected ascospores may be caught on dry glass coverslips suspended at distances of the order of 1 mm vertically above

perithecia discharging in a still atmosphere. When perithecia discharge into air, invariably groups of eight spores are collected, indicating that all the spores of each ascus are released simultaneously. The unit of dispersal from the perithecium thus is not the single spore but the whole contents of an ascus, the eight spores remaining together presumably because of a sticky mucilaginous surface coating which also enables them to adhere to dry glass and other substrates from which they are not readily detached without wetting. If spore groups on a dry glass surface are moistened slightly, e.g. by breathing on a slide, the spores of each group immediately separate within a small water droplet and it is clear that they are no longer contained within an ascus wall.

Direct observations of falling ascospore groups over a measured interval within a closed glass tube have shown that these have a settling velocity of approximately 4 mm/sec. This figure agrees closely with the calculated value of 3·8 mm/sec derived from substitution in Gregory's (1945) equation $V = 0{\cdot}0121\, r^2$. (V = terminal velocity in cm/sec, r = effective radius in microns.)

Table 1

HAEMACYTOMETER COUNTS OF E. ARMENIACAE ASCOSPORES AT INTERVALS AFTER IMMERSING IN WATER A 1 CM SQUARE SPECIMEN OF PERITHECIAL STROMA

Time from immersion (hr)	$2\frac{1}{4}$	$4\frac{1}{4}$	$7\frac{1}{4}$	$23\frac{3}{4}$	$28\frac{3}{4}$	48
Total ejected (10^9 spores)	2·7	3·4	4·8	6·3	8·5	10·4

(iii) *Relationship between Ascospore Discharge and Weather Conditions*.—An impactor unit was constructed from "Perspex" according to the specifications of Gregory (1954) and preliminary tests for efficiency of trapping ascospore groups of *E. armeniacae* were made in a wind tunnel. With a thin film of petroleum jelly applied to the slide, the impactor proved highly effective when operated at a flow rate of approximately 10 l/min.

The high rate of "gummosis" infection known to occur in the Adelaide metropolitan area (84 per cent. of trees infected according to Grace's survey, 1949) suggested the presence of abundant inoculum at appropriate times. Sampling therefore was done under varying weather conditions at the site of the meteorological instruments at the Waite Institute, which is situated on rising ground with several miles of suburbs (containing a large scattered population of apricot trees) lying to the south-west, west, and north-west. The prevailing winds during rainy weather are from these directions and the site was considered an ideal one for gaining information about ascospore movement under various weather conditions. Samples were taken with the impactor unit operating approximately 4 ft 6 in. above ground level, and suction was provided by a filter pump attached to a nearby water tap. Isokinetic sampling was not attempted owing to variations in both wind speeds and

suction rates (the latter caused by water pressure fluctuations) but a suction rate of approximately 10 l/min was maintained as far as possible.

The data for six different sampling runs are presented in Table 2, and it is seen that ascospores of *E. armeniacae* were not detected in the atmosphere when there had been less that 0·05 or 0·06 in. of rain during the 5 hr prior to the sampling period, nor were they detected unless some rain had fallen within the 2 hr immediately prior to the sampling period.

Table 2

SPORE COUNTS AND RELEVANT METEOROLOGICAL DATA FOR SLIDE EXPOSURES ON SIX SEPARATE DAYS

Date	Rainfall in 5 Hr Preceding Sample Period (in.)	Time since Rain Fell at Beginning of Sample Period (hr)	Sample Period	Wind Direction	Approx. Volume Sampled (l.)	Approx. No. of *E. armeniacae* Groups per m^3
14.vii.55	Nil	5½	10·18–10·48	SW.	300	Nil
	Nil	6	10·50–11·28	SW.	280	Nil
	Nil	6½	11·28–11·58	SW.	300	Nil
	Nil	7	11·58–12·28	SW.	300	Nil
26. ix.55	0·32	1¼	14·35–15·32	W.	450	7
27. ix.55	0·01	¼	11·33–12·33	SW.–S.	600	Nil
6. x.55	0·05	½	9·34–10·39	NE.–N.	520	Nil
	0·05	1½	10·40–11·40	NE.–N.	540	Nil
	0·05	2½	11·42–12·42	N.	540	Nil
7. x.55	0·16	Light rain during sampling	9·24–10·24	SW.	600	2
	0·16		10·25–11·41	SW.–S.	760	1–2
	0·09		11·45–14·04	SSW.–S.	1700	3
	0·06	½	14·06–15·31	SSW.–S.	800	6
	0·05	2	15·32–16·32	SSW.–S.	600	2
28. x.55	0·16	Light rain during sampling	14·53–16·31	Variable almost no wind	800	25

As regards spore numbers, more recent samplings taken under comparable weather conditions during the autumn of 1956 have yielded counts ranging from 0–2 per cubic metre which are considerably lower than those recorded under favourable conditions during the previous spring (see Table 2). Similar numbers (0–3/m^3) have been recorded at Nuriootpa (the centre of one of the worst-affected districts in South Australia) during May and June 1956, but no previous samples have been taken in this district.

(iv) *Viability of Ejected Ascospores.*—The only available information has been provided by laboratory tests in which ascospores were discharged directly on to clean dry glass slides and the percentage of spores germinable on 1 per cent. distilled water agar determined after intervals during which the slides were kept in air on the laboratory bench. Viability data are presented in Table 3.

Table 3

VIABILITY OF EJECTED ASCOSPORES OF E. ARMENIACAE AFTER STORAGE ON DRY GLASS SLIDES IN AIR

Time Stored (days)	Ejected 4.v.55		Ejected 21.ix.55		Ejected 14.xi.55	
	Approx. % Germination	Time to Germinate (hr)	Approx. % Germination	Time to Germinate (hr)	Approx. % Germination	Time to Germinate (hr)
0	100	12–14				
7			95	12–16		
14			62	12–18	92	12–16
15	90					
19	90	18				
20	90	18–24				
21			47	20–24		
26	50	21				
28			15	48–72	85	12–16
34	2	24–48				
35			4	48–72	77	18–20
42			37	24–48		
49					44 (8)*	20–22
56					57 (0·5)	24
63					Nil	
70					13 (Nil)	48

* In some instances, duplicate slides gave widely separated germination percentages: these are given in parentheses.

From the data of Table 3, it is evident that ejected ascospores of *E. armeniacae* may have an extremely long life under suitable conditions. In these tests, atmospheric temperatures in the laboratory ranged between 15°C (winter) and 35°C (summer); although other factors undoubtedly play a part under field conditions, there is reason to believe that these spores have sufficient longevity to survive air dispersal over long distances.

(v) *Conclusions.*—From the foregoing evidence, it is clear that ascospore discharge may be expected whenever a rain greater than about 0·05 in. falls on mature perithecia, and that discharge from any perithecium may continue intermittently for several months and possibly for more than one rainfall season. Preliminary observations indicate that a peak discharge may occur in spring and that only very low spore numbers are encountered during other seasons; this

suggests that the normal discharge life of most perithecia is completed during the season following their maturity and that a fresh crop of perithecia reach maturity in the spring of each year.

(e) *Infection Phase of the Disease*

(i) *Temperature Requirements for Ascospore Germination.*—Determinations were made by incubating freshly ejected ascospores of *E. armeniacae* on 1 per cent. distilled

TABLE 4

GERMINATION TIME OF E. ARMENIACAE ASCOSPORES ON DISTILLED WATER AGAR AT A SERIES OF TEMPERATURES

Temperature		Time to Germinate (hr)	Remarks
Max. Observed (°C)	Min. Observed (°C)		
2	0·5	>160	Transferred to room temperature after 187 hr and germinated in 5 hr
8	6·5	65	
12	10·5	41	
15·5	13·5	16–29	
18·5	16·5	16	
20·5	18·5	12–16	
22·5	20·5	11·5	
25	23	11·5	
27	25·5	12–16	
30	28	12–16	
32·5	31·5	41	
36	35	—	Failed to swell in 65 hr and plates transferred to 25°C.; failed to germinate or swell in the next 100 hr
41	40	—	Failed to swell in 65 hr and plates transferred to 25°C.; failed to germinate or swell in the next 100 hr
46	44	—	Failed to swell in 41 hr and plate transferred to 25°C.; failed to germinate or swell in the next 120 hr

water agar in petri plates at a range of temperatures between 1 and 45°C in a multiple-temperature incubator. Compartment temperatures were read once daily and the maximum and minimum recorded for each compartment over the duration of the test; these, together with the number of hours before the majority of spores were showing germ tubes at the corresponding temperatures, are given in Table 4.

The optimum temperature for germination was 22–25°C and germination time increased markedly on either side of this range. Ascospores imbibed water and were able to withstand at least 7 days at temperatures just above 0°C, but neither water uptake nor germination occurred at or above 35°C.

(ii) *Moisture Requirements for Ascospore Germination.*—Germination tests were made by incubating ascospores, which had been ejected directly on to clean dry glass slides, in sealed Coplin jars at a range of atmospheric humidities at 25°C. Represen-

tative relative humidities from 30 to 100 per cent. were obtained by using saturated solutions of appropriate chemicals selected from O'Brien's (1948) list.

E. armeniacae ascospores required at least 90 per cent. relative humidity for germination, and above this critical level germination took place in 1–2 days. The highest percentage germination occurred at a relative humidity of 96·6 per cent. over a saturated solution of potassium dihydrogen phosphate.

(iii) *Measurements of Natural Field Infection.*—A field experiment in a block of young unpruned apricot trees at Fullarton was run for a 12-month period during 1954–55 as follows: a series of 20 wounds similar to normal pruning cuts was made every 4 weeks at predetermined and randomly allocated positions. Each series of wounds was left exposed for 4 weeks and then covered with tinfoil and surgical bandage to prevent further access of spores. By this means it was hoped to gain a measure of the amount of natural infection occurring during each 4-week period for a year, but certain limitations were recognized, namely:

(1) The impossibility of distinguishing between the effects of seasonal variations in wound susceptibility, abundance of inoculum, and meteorological conditions favourable for infection, all of which would influence the number of infections recorded for any 4-week period; and,

(2) The likelihood of creating conditions more favourable for spore germination and infection by covering the wounds. This factor might influence absolute numbers but should not affect relative numbers of infections.

Because of these limitations, the results require cautious interpretation. The numbers of infections recorded are undoubtedly higher than those which normally occur on uncovered wounds, but they provide useful comparative data which may be analysed with the concurrent weather conditions. In Table 5, which has been condensed from more detailed data, are shown infection scores, numbers of days on which ascospore discharge could be expected, and "mean wet-day temperatures" (calculated from recorded maxima and minima on days on which rain fell), for each 4-week period from August 2, 1954 to August 1, 1955.

From the data of Table 5, it is seen that no infections were recorded between mid April and the end of August although these months contained the highest proportion of days conducive to ascospore discharge. Infection peaks occurred in spring (October) and late summer (February March). During the autumn-winter period in which no infections were recorded, mean wet-day temperatures were all below 60°F and all but one below 55°F. Two hypotheses can be advanced to explain these observations.

First, it has been shown that free moisture or a relative humidity of at least 90 per cent. is essential for ascospore germination and that the time required for germination depends on the temperature. The data of Table 4, which may be interpolated to give information on intermediate points, show that the germination time at 51°F (10·6°C) is approximately 48 hr, and not until the temperature rises to 60°F (15·6°C) is this period reduced to 24 hr. Thus during the winter months humidity must remain above the critical level for at least 2 days if infection is to take place, whereas half this time would suffice in warmer weather. It is thought

that the chances of a continued period of sufficiently high humidity during these cold months would be a rare event, and that, if sufficient moisture were supplied by continuous rain over a 2-day period, most spores would be washed from the infection courts.

Secondly, spore-counts made at different times during the past 12 months have suggested that numbers during winter are extremely low and rise to a peak in spring, but further data are required before the seasonal distribution can be assessed accurately. In the opinion of the author, both of these factors are likely to account for the observed low incidence of infection in winter.

Table 5

METEOROLOGICAL DATA AND NATURAL "GUMMOSIS" INFECTIONS RECORDED ON WOUNDS EXPOSED AT THE FULLARTON ORCHARD FOR 4-WEEK PERIODS DURING 1954–55

Exposure Period	No. of Days Discharge Expected	Mean Wet-day Temperature (°F)	No. of Infections (possible 20)
2.viii.54–30.viii.54	7	52	Nil
30.viii.54–28. ix.54	6	57	2
28. ix.54–25. x.54	6	60	9
25. x.54–22. xi.54	6	65	1
22. xi.54–20. xii.54	3	71	1
20. xii.54–17. i.55	Nil	—	Nil
17. i.55–14. ii.55	2	70	2
14. ii.55–14. iii.55	1	71	5
14. iii.55–12. iv.55	3	78	2
12. iv.55– 9. v.55	8	58	Nil
9. v.55– 6. vi.55	14	54	Nil
6. vi.55– 4. vii.55	11	54	Nil*
4. vii.55– 1.viii.55	7	51	Nil

* Possible 19.

(iv) *Conclusions*.—Evidence from laboratory germination tests under a range of temperatures and relative humidities, and from natural infection studies in the field, leads to the conclusion that most infections take place during the September–November period, at which time high atmospheric spore numbers have been recorded. Under normal orchard practice, the current year's pruning wounds would then be 1–5 months of age. As no data are available for the age limit of wound susceptibility, it is not possible to relate to normal practice the "autumn peak" of infections recorded in a field experiment.

IV. Pathogenicity to Other Hosts

Adam (1938) and the present author have noted the occurrence of "gummosis" disease in prunes (*Prunus domestica* L.), and isolates of *Cystosporina* from prune

lesions have been proved pathogenic to apricot. The author has examined many similar lesions on peach (*Prunus persica* L.) but has never detected the presence of *Cytosporina* in them. Perithecia of *E. armeniacae* have not been found on the wood of any species other than *P. armeniaca*.*

During 1953, the writer inoculated 98 different varieties of *P. persica* (peach and nectarine) and one plum variety (Golden Drop) with mycelium of *Cytosporina* isolates known to be pathogenic to apricot, using the method described in Section III. All varieties developed symptoms of "gummosis" infection within 3–6 months, and isolations from a number of these showed that the fungus had penetrated the wood for distances comparable with those found in apricot inoculations of similar ages. Pathogenicity of the reisolated fungus was confirmed in all cases by inoculation to apricot.

In 1955, one peach seedling in the glass-house was successfully inoculated with ungerminated ascospores of *E. armeniacae*. The spores were applied to freshly made wounds in July and incubated with moist wicks for 1 week. *Cytosporina* was recovered in April 1956 and its pathogenicity confirmed by inoculation to apricot.

It is thus evident that *Cytosporina* or *Eutypa* mycelium can grow in the wood of *Prunus* species outside its natural host range, but normally it is unable to gain entry. Under special conditions of incubation, however, ascospores of *E. armeniacae* were able to germinate and penetrate a freshly made wound on a peach seedling.

V. Discussion

For many years *Cytosporina* sp., the causal organism of apricot "gummosis", has been a pathogen of major economic importance to the horticultural industry in southern Australia, and the development of adequate control measures has been hindered by lack of knowledge of its life-cycle and transmission.

The results of experiments described in Section III show clearly that *E. armeniacae* is an active "gummosis"-inciting pathogen and that the distribution of its perithecia in southern Australia coincides with that of the disease. Strong evidence is produced in support of the hypothesis that *E. armeniacae* and *Cytosporina* sp. are stages in the life-cycle of a single organism, and that airborne ascospores constitute inoculum by which "gummosis" disease is spread.

The author is of the opinion that insufficient ascosporic inoculum is produced in the low-rainfall irrigated districts of South Australia to account for the amount of infection occurring, as only two tree butts bearing perithecia have been located after extensive searching. There are only two possible alternative sources of infection for trees in these districts: airborne inoculum from other districts or transmission by other means. Adam (1938) was able to demonstrate pruning-saw transmission experimentally, but this is unlikely to account for more than the odd infection in practice. The role of the pycnospores has been the subject of much speculation by previous investigators, some of whom (Holloway, unpublished data 1950; Adam, Grace, and Flentje 1952) claimed that these were capable of transmitting the

* Since this paper was accepted for publication, the author has detected perithecia of *E. armeniacae* on dead wood of *Vitis vinifera* L. in a number of South Australian vineyards; detailed investigations are proceeding.

disease. The author has been unable to germinate these on any of a wide variety of media, and, whilst the possibility of infections arising from pycnidial *hyphae* rather than from the spore component of the pycnidial tendrils has not been overlooked, it seems certain that transfer could only be effected between closely adjacent tree limbs. The pattern of disease seen in orchards in no way supports such a hypothesis.

The nature and viability of ejected ascospores make long distance transmission theoretically possible. The maximum distance of the nearest abundant source of ascospores from any of the upper Murray irrigation settlements in South Australia is 100 miles, and the author believes that airborne inoculum from districts such as the Barossa Valley produces many of the infections which occur in the irrigated settlements. No evidence is yet available to substantiate this belief, but information is being sought by sampling the air spora at appropriate times and sites.

To the east and north-east of the South Australian irrigation settlements lie some hundreds of miles of low-rainfall country where no apricots are grown. This natural ecological barrier offers a logical explanation for the very low incidence of "gummosis" disease reported by Grace (unpublished data 1949) in the Murrumbidgee irrigation districts of New South Wales. These districts have not been visited by the author and there is no information about local sources of inoculum there.

Many Ascomycetes require a fusion of complementary mating-type mycelia before fertile perithecia can be produced, but whether this is the case with *E. armeniacae* will not be known until it is possible to produce perithecia under controlled conditions in the laboratory. If the species is heterothallic, then considerable survival advantage could be attributed to its method of dissemination. The majority of infections are likely to result from germination of more than one spore, thus increasing the potential for perithecial formation and abundance of inoculum for further propagation.

Spread of "gummosis" disease undoubtedly has been aided by concurrent horticultural practices. Of these, the most significant are heavy pruning systems which make many potential infection courts each year and the common habit of allowing infected dead limbs to remain in and near orchards. With regard to the former, Smith (1953) has shown that the disease is virtually absent from apricot trees which have never been pruned, and the author's own observations in the Hobart district of Tasmania lead to the conclusion that faulty hygiene combined with extremely favourable climatic conditions for *Eutypa* fructification have there produced the highest density of infective material seen in southern Australia.

VI. Acknowledgments

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Thanks are due to Dr. C. G. Hansford and Dr. N. T. Flentje for helpful advice; to Department of Agriculture Officers in the States concerned for assistance in the

AN AIRBORNE VASCULAR PATHOGEN OF PRUNUS ARMENIACA

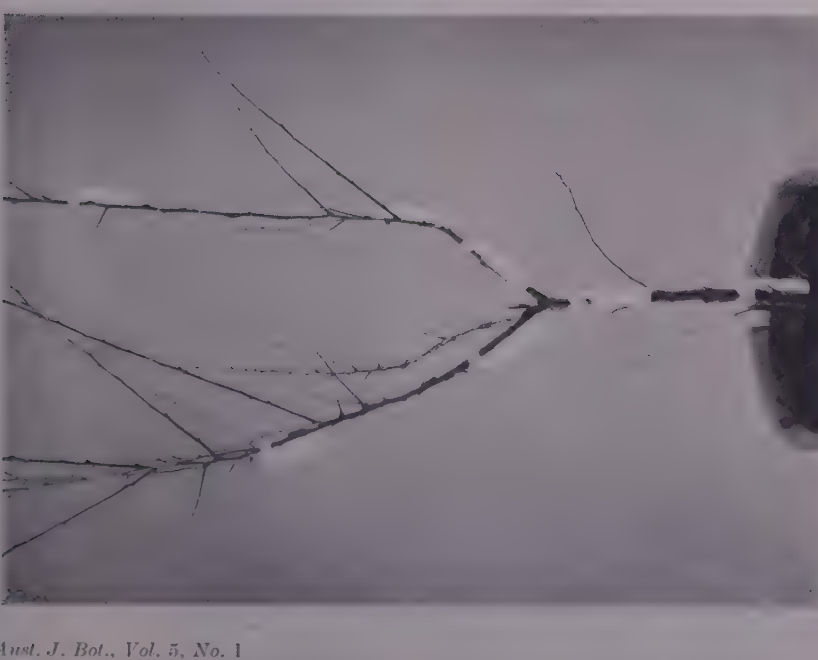

Fig. 1.—Two-year-old apricot seedling inoculated with ascospores of *E. armeniacae*, May 1955.

Fig. 2.—Same apricot seedling photographed in October 1955 after collapse of a limb.

field; and to the Education Department of South Australia for the use of apricot trees in the Fullarton Orchard.

Dr. N. H. White, University of Sydney, kindly supplied certain cultures to which reference has been made; the spore impactor unit was constructed at the Waite Institute by Mr. K. J. Barrow; and photography was by Mr. K. P. Phillips.

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THE RELATIVE ABUNDANCE OF *MORTIERELLA* COEMANS SPP. IN ACID HEATH SOILS

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Summary

The fungal population of two podzolized heath soils, one with and one without a hardpan, is characterized by a marked contrast in the species distribution of the genus *Mortierella* Linnemann. The dominant species in the hardpan soil is *Mortierella ramanniana* (Möll) Linnemann, but when the pan is lacking it is replaced by *Mortierella nana* Linnemann. This is not a local effect, for an analysis of results from comparable English soils gives a parallel result. It can be stated that the dominance of one or other of these species is indicative of certain *soil types*.

I. Introduction

The vegetation at Frankston (Victoria, Australia) is described as heath; scattered through it are clumps of stunted *Eucalyptus viminalis* Labill. This plant community occurs on a podzolic soil known as *Cranbourne sand* (Leeper 1948). It is an acidic deep sand in which the A_{00} layer is represented by a scatter of leaves etc. from the sclerophyllous heath flora, while the A_0 horizon of decomposing humus material is not apparent. The A_1 horizon is sandy, dark grey in colour from the included organic material. The A_2 is of similar texture, but light in colour, for it has been leached of the organic material. The A_2 passes abruptly into the B horizon, which is characterized by its intense brown to black colour. It consists of a dark brown sandstone cemented together with an accumulation of humus material and iron compounds, pan-like in character, and often referred to as "coffee-rock" or ortstein. It is a narrow layer horizontally, but it runs deeply into the C horizon of deep yellow sand in the form of vertical cylinders, the centres of which are occupied by corresponding downward extensions of the A_2 layer (Stephens 1953).

At Anglesea, Vic., the vegetation is of a similar heathy type, but natural tree growth is more abundant. When this area is planted with *Pinus* spp. the infertility of these soils is apparent, and addition of superphosphate is required before they can be put to any economic use. The Victorian Forests Commission has an area in this region where experimental planting is under observation.

The soil in general is referred to as *Angahook fine sand*. In the experimental area of Plantation 1, in contrast to the Cranbourne sand profile, the profile shows 2 ft of fine sand overlying a yellowish-grey heavy clay, the transition to the underlying clay is sharp and there is no development of coffee-rock. In other parts of the Forestry area an incipient coffee-rock may be present, and at still other sites a typical coffee-rock layer may occur. The C horizon, in contrast to the Cranbourne sand, is in all cases the yellowish grey heavy clay.

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When a comparison was made of the fungi isolated from areas lacking the characteristic coffee-rock with those isolated from the coffee-rock areas, a striking difference was noted between the fungal populations. This difference lies chiefly in the species representation of the genus *Mortierella*. It is suggested that this difference is not a local one, but that it occurs in the northern hemisphere in somewhat comparable soils, and it leads one to postulate that the dominance of one or other of the species of this genus is indicative of certain soil types.

TABLE 1

THE NUMBER OF PLATES PREPARED FROM ANGAHOOK FINE SAND WITHOUT A HARDPAN, ON WHICH SPECIES OF MORTIERELLA, TRICHODERMA, ASPERGILLUS, AND PENICILLIUM APPEARED

Sample*	No. of Plates	No. of Plates on which Present									
		Mortierella		*Trichoderma*	*Aspergillus*			*Penicillium*			
		M. nana	*M. isabellina*	*T. viride*	*A. terreus*	*A. fumigatus*	*A. nutans*	*P. ochraceum*	*P. nigricans*	*P. funiculosum*	*P. janthinellum*
1	24	13	—	21	1	4	—	10	17	3	9
2	24	19	—	11	4	3	1	14	5	2	6
3	24	18	—	18	11	—	4	8	10	2	5
4	24	21	—	12	1	—	6	9	13	2	10
5	32	30	6	12	15	1	7	17	1	16	—
6	32	32	11	11	11	4	5	21	5	12	—
7	32	31	6	23	6	5	1	19	15	15	4
8	31	30	3	22	21	1	3	13	7	7	14
	223	194	26	130	70	18	27	111	73	59	48

* Samples 5–8 treated by the method of Rose and Muller.

II. Methods

The method of sampling was similar to that used by the authors in a study of the ecology of the fungi in the Frankston heathland soils (McLennan and Ducker 1951). In some later experiments the method of sampling was altered and the procedure followed that recommended by Rose and Muller (1954) working with New Zealand pasture soils.

III. Results

It has been shown previously (McLennan and Ducker 1951, 1954) that the density of *Mortierella ramanniana* (Möll.) Linnemann in Frankston podzols ranges between 79 and 89 per cent. in the A and B horizons. *Penicillium*, with a great variety of species, ranks next with a density of 16 per cent.

TABLE 2

THE NUMBER OF COLONIES OF M. NANA AND OTHER FUNGI APPEARING ON DILUTION PLATES OF ANGLESEA SOIL LACKING A COFFEE-ROCK LAYER

Sample	No. of Plates	*M. nana*		*T. viride*		*Penicillium* spp.		*Aspergillus* spp.		Other Genera	
		No. of Plates on which Present	No. of Colonies	No. of Plates on which Present	No. of Colonies	No. of Plates on which Present	No. of Colonies	No. of Plates on which Present	No. of Colonies	No. of Plates on which Present	No. of Colonies
1	36	21	90	19	23	23	76	11	21	5	10
2	24	21	144	12	16	22	91	11	19	6	9
3	32	31	200	13	14	31	177	17	48	4	6
	92	73	434	44	53	76	344	39	88	15	25

In the Anglesea soil, *lacking a hardpan, M. ramanniana* is not found on the dilution plates. Its place is taken by another species of the genus, *Mortierella nana* Linnemann. Typical of results obtained throughout the authors' work are those illustrated by the following two experiments. See also Tables 1 and 2.

Experiment 1

The density of *M. nana* is given by:

(Total number of *M. nana* colonies/Total number of colonies on the plates) $\times 100$

$$= (145/287) \times 100$$
$$= 50{\cdot}5 \text{ per cent.}$$

The frequency percentage is given by:

(Number of samples of occurrence/Total number of samples) $\times 100$

$$= (21/24) \times 100$$
$$= 87{\cdot}5 \text{ per cent.}$$

Fungal counts from soil made from dilution plates from samples from the same area generally show variations. Rose and Muller (1954) working with New Zealand pasture soils found such variations to be of the order of 1 : 13. They considered that the main source of error between mean counts is the variation between the core samples; the variations from subsampling and plating methods were of a much lower order. Their method requires as many as 25 cores per field, and, as the samples were bulked in this work, 32 cores were finally taken in each experiment. As will be seen, the results show a close approximation irrespective of the method of sampling (Table 1).

Experiment 2 (sampling by Rose and Muller method)

	M. nana	All *Penicillium* spp.	*Trichoderma viride* Pers.
Density (%)	50·9	30·5	8·4
Frequency (%)	96·9	96·8	43·7

When a hardpan (coffee-rock) is present in the profile at Anglesea the fungal picture changes, insofar as *M. nana* no longer appears on the plates, its place being taken by *M. ramanniana* (Table 3).

From a site at Anglesea where a coffee-rock layer is present dilution plates were prepared. A detailed examination of all the colonies on the plates was not attempted. Attention was directed to the *Mortierella* colonies, so it is not possible to calculate density and frequency in this experiment. The results are expressed as percentages of colonies on each plate. Plates from samples taken at 1–6 in. showed *M. ramanniana* in every plate, and no colonies of *M. nana* were recorded. At 3 ft 6 in. (coffee-rock), of six plates, three gave 100 per cent. *M. ramanniana* colonies and three averaged 73·3 per cent. In all ways the population on the plates from this and similar sites resembled the population of the Frankston podzol.

If a hardpan (coffee-rock) is present, then *M. ramanniana* is the dominant form in the profile; if the pan is lacking, *M. nana* replaces it. In our experience this

is so characteristic a phenomenon that these two fungi serve as criteria for the type of sandy podzolic soil (i.e. coffee-rock or hardpan present or absent).

The pH of the soils samples ranged from 3·50 to 4·65.

(*a*) *The Genus* Mortierella *Coemans in the Acid Heath Soils*

The species of *Mortierella* isolated by the authors from the Cranbourne and Angahook sands are *M. isabellina* Oudemans, *M. nana* Linnemann, *M. pusilla* Oudemans, *M. ramanniana* (Möll.) Linnemann, *M. stylospora* Dixon-Stewart, and *M. vinacea* Dixon-Stewart. (Dixon-Stewart 1932; Linnemann 1941.)

TABLE 3

THE EFFECT OF THE PRESENCE OR ABSENCE OF A HARDPAN ON THE OCCURRENCE OF MORTIERELLA SPECIES IN ACID SANDY PODZOLS

Sample No.*	Coffee-rock Present		Coffee-rock Absent	
	M. ramanniana	*M. nana*	*M. ramanniana*	*M. nana*
1	+++	.	.	+++
2	++++	.	.	++
3	++	.	.	+++
4	++++	.	.	+++
5	++++	.	.	+++
6	++++	.	.	++

* Cores were taken at depths varying from 1 to 26 in. and then bulked before sampling.

With the exception of *M. nana* and *M. ramanniana*, their occurrence in these soils is more or less sporadic. *M. isabellina* appeared 39 times and *M. stylospora* 20 times in a total of 236 plates. *M. pusilla* and *M. vinacea* were much less frequent.

The isolations of *M. ramanniana* varied in colour and depth of turf as well as in spore size; further work on this species is in progress. All the species have been previously recorded as present in Australian soils except *M. nana*. Isolations of this species from Anglesea were sent to Professor Linnemann for authentication. She agreed with the authors' identification, and in correspondence suggested to us that, not only was this the first record of the species for Australia, but that it was also the first record of its occurrence in soils outside Germany.*

Jeffreys *et al.* (1953), interested in the antibiotic production by fungi in acid heath soils in England, studied soils derived from Bagshot sands. All were highly acid, the majority were well-developed podzols, but some rested directly on the subsoil without a pan.

Reference to Table 4, adapted from results set out in their paper, reveals a most striking parallel with the Australian results—the dominance of *M. ramanniana*†

* A paper (Chesters and Thornton 1956) has just become available in Australia, in which *M. nana* is recorded as present in British soils.

† Jeffreys *et al.* quote this fungus as *Mucor ramannianus*.

TABLE 4

THE EFFECT OF THE PRESENCE OR ABSENCE OF A HARDPAN IN ENGLISH ACID SANDY PODZOLS ON THE SPECIES OF MORTIERELLA

pH ranged between 4 and 5. +++ = abundant; ++ = frequent; + = rare; . = absent

Sample No.	Depth (in.)	Surrey, Iron Pan Present									Dorset, Iron Pan Present			Dorset, No Iron Pan					
		Poor Heath (*Calluna*)			Poor Heath			Thick Heath			Good Stand Scots Pine			Young Scots Pine			Felled Poor Pine Heath Cover		
		Horizon	*M. ramanniana*	*M. alpina*	Horizon	*M. ramanniana*	*M. alpina*	Horizon	*M. ramanniana*	*M. alpina*	Horizon	*M. ramanniana*	*M. alpina*	Horizon	*M. ramanniana*	*M. alpina*	Horizon	*M. ramanniana*	*M. alpina*
1	0–1	A_1	+	.	A_1	.	.	A_1	.	.	A_0	++	+	A_0	.	+	A_0	.	+++
2	1–2	A_1	++	.	A_1	++	.	A_2 (samples 2–3)	++	.	A_0	.	.	A_1	.	+	A_1	.	.
3	2–4	A_2	+++	.	A_2	+++	.				A_1	+	.	A_1	.	.	A_1 (samples 3–4)	.	+
4	4–8	A_2	+++	.	A_2	+++	.	A_2	+++	.	A_2 (samples 4–5)	+++	.	A_2	.	+++			
5	8–10	B	+++	.	B	+++	.	A_2 (samples 5–6)	+++	.				A_2 (samples 5–6)	.	.	A_2 (samples 5–6)	.	.
6	10–12	B	++	.	C	+++	.				B	+++	.						
7	12–16	C	.	.	C	++	.	B	+++	.	B (12–13 in.)	+++	.	C	.	.	C	.	.
	or 16–17							C	+++	.	C (13–18 in.)	+	.				C	.	.

in the iron pan profiles and its absence when the A_2 horizon grades imperceptibly into the C horizon—a reddish brown sand. The English workers noted that this species was an abundant and characteristic feature in six of the nine profiles they studied, and that it was completely absent in three: "This might be related to the occurrence of a well-marked iron pan in the B horizon, for in all such profiles *M. ramanniana* was present, in those with an ill-defined B horizon it was absent. This may have been purely fortuitous but is worthy of record." Again: "*M. ramanniana* was most commonly found in the lower levels of the A horizon and in the B horizon, even occurring abundantly in the C horizon in some profiles. In some samples *it was present in almost pure culture.*"

IV. Discussion

An analysis of the literature suggests that the fungal flora of the soil is remarkably uniform, irrespective of soil type, and that except for certain general trends, e.g. the replacement of *Penicillia* by *Aspergilli* in the tropics, this uniformity is world-wide.

Table 5

The effect of pH on the range of three fungi found in the Breckland heath soils (adapted from Burges)

Tolerance	Soil Type	A	B	C	D	E	F	G
	pH	8·20	7·81	6·18	4·36	3·95	3·77	3·70
Tolerant	*Trichoderma viride*	+	+	+	+	+	+	+
Acid range	*M. ramanniana*	−	−	−	−	++	++	++
Exacting	*P. janthinellum*	++	++	+	−	−	−	−

As Burges (1953) points out: " . . . to anyone familiar with the ecology of the higher plant, this idea of uniformity seems strange when one considers the mosaic of plant communities which are closely correlated with different soils and habitats".

Generically the soil fungi are a cosmopolitan group, but, when a detailed study of the species of fungi present in soils is made, then it is realized that this uniformity is not so evident.

The Breckland heath area in East Anglia, within an expanse of a few square miles, shows a wide range of soils. Although all have developed from the same chalky-boulder clay, progressive leaching has given soil types designated by Watt (1940) as types A–G. Of these soil types D–G are acid soils, owing to the leaching of the chalk, and these soil types carry *Calluna* heath. Soils F–G are well-developed podzols. Burges, studying these soils, found that he could divide the fungi occurring on the plates into three groups, according to their pH tolerance (Table 5).

From these and similar results Burges concludes that ecologically fungi behave as any other group of plants; some extended through the range of soils, some were limited to soils of high base status (cf. Watt's exacting species), while still others were found only in the acid range.

Lists of fungi isolated from soil have tended in the past to support the view that as a group they showed a uniform cosmopolitan distribution. Generically this does seem to be the pattern. More detailed study of the species distribution and attention to the density and frequency of occurrence of particular species throws new light on this generalization. The replacement of *M. ramanniana* by *M. nana* in certain Australian soils, and a similar replacement of two species of *Mortierella* in comparable English heath soils are excellent examples of this variation of fungal types in closely parallel soils.

Christensen, working with podzolic soils of conifer hardwood communities in Northern Wisconsin, states in correspondence, that the species list which has been compiled for these soils shows a striking similarity to the species list published by the authors (McLennan and Ducker 1954) for acid sandy podzols in southern Australia and those published by Jeffreys *et al.* (1953) for podzolic heath soils in England. The important mucoraceous forms in Wisconsin are again *M. ramanniana*, *M. isabellina*, and *M. vinacea*.

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A STUDY OF SOME SOIL PROPERTIES IN RELATION TO THE INVASION OF NATIVE PASTURES BY *BOTHRIOCHLOA AMBIGUA* S. T. BLAKE.

By C. W. E. Moore*

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Summary

Soil samples at 1-in. intervals to a depth of 6 in. were obtained from six paired stands of *Bothriochloa ambigua* S. T. Blake and of *Danthonia* spp. at each of three sites.

Determinations of moisture equivalent, pH, and total nitrogen were made on all samples, organic carbon on the 0–1 in. samples, and mechanical analyses on the 0–1 in., 4–5 in., and 5–6 in. samples.

Significant differences were found between the soils of the two communities in moisture equivalent, organic carbon, and per cent. silt + clay at 0–1 in.; in pH at 0–1 in., 3–4 in., and 5–6 in.; and in total nitrogen at all depths except 4–5 in.

The results are discussed in relation to the effect of *B. ambigua* on the soil and the possibility that certain soil conditions favour invasion of native pastures by this species.

I. Introduction

Bothriochloa ambigua S. T. Blake is a prominent constituent of the native pastures of the Southern Tablelands and south-western slopes of New South Wales. It is also commonly found as the dominant species in the pastures over large areas in the New England region (Roe 1947). In the latter district Roe (1947) states that it is "a vigorous colonizer of cultivation that is allowed to revert to pasture, as well as a strong invader of the natural sward." Moore (1953) suggested that *B. ambigua* invades *Danthonia*-dominant pastures following weakening of the sward through over-grazing and subsequent erosion of the surface soil. This view was supported by the frequent occurrence of *B. ambigua* as the dominant species on roadsides where the surface soil had been removed in the process of road construction, while *Danthonia* spp. remained dominant in undisturbed areas.

The work reported here compares certain properties of the soils from stands of *B. ambigua* with those of the soils of neighbouring stands of *Danthonia*. Invasion of the native pastures by *B. ambigua* appears to be followed by marked changes in the soil properties studied.

The species of *Danthonia* found on the sites studied are *D. pilosa* R.Br., *D. auriculata* J. M. Black, and *D. carphoides* F. Muell. ex Benth. At site *C*, *D. caespitosa* Gaud. *in* Freycinet also occurs. An important factor influencing the proportion of the various species of *Danthonia* at any particular site is the grazing pressure. *D. pilosa* and *D. caespitosa* are more susceptible to heavy grazing than are *D. auriculata* and *D. carphoides*.

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II. Climate and Soils

Climatological data for the Southern Tablelands have been published by the Commonwealth Bureau of Meteorology (1948). The following summary of the climatic conditions is based on the records for the Australian Forestry School, Canberra.

Mean monthly rainfall is nearly uniform throughout the year (approximately 2 in. per month), but owing to high temperatures evaporation during the summer greatly exceeds the precipitation, and rain during this season is relatively ineffective. During the winter temperatures are low and, though the moisture supply may be adequate, plant growth is retarded. Prescott and Thomas (1949) have suggested that the value of $P/E^{0 \cdot 75}$ may give a reliable indication of the moisture supply in relation to the requirements of different plants. This value is less than $0 \cdot 4$ during December, January, and February, which includes the period of active growth of *B. ambigua*. Only during summers of above average rainfall can this species develop fully and produce seed, though established plants are capable of persisting through hot, dry summers.

The soils on the sites chosen for this study have been classified as podsolics (Prescott 1952), grey-brown podsolics (Costin 1954), and red and yellow podsolics (Stephens 1950). Downes (1954) has suggested that they had an earlier history of salinization and should be regarded as solodic soils.

The soils are derived in part from igneous rocks (granite and porphyry) and in part from sedimentary rocks (shales and sandstones). In general, the surface soil is a loam to silty loam, usually with a bleached A_2 horizon. The B horizon is a medium to heavy mottled clay, with quartz gravel where the parent material is granite or porphyry. The transition from A to B horizons is gradual in those soils derived from igneous rocks, but sharp where the parent material is sedimentary.

III. Methods

Three sites were chosen in which native pastures previously dominated by *Danthonia* spp. had been to some extent invaded by *B. ambigua*. Sites *A* and *B* are located 18 miles from Canberra on the Canberra–Yass Road, and site *C* near Gunning on the Hume Highway. The soil parent materials of sites *A* and *B* are porphyry and sedimentary rocks, while at site *C* the soil is derived from granite.

At each site six stands of *B. ambigua*, and for each of these a neighbouring stand of *Danthonia* on the same contour, were selected. Within each stand soil samples were obtained in September 1953 at 0–1 in., 1 2 in., 2–3 in., 3–4 in., 4–5 in., and 5–6 in.To reduce inherent soil variation as far as practicable, the samples from each pair of communities were taken on the same contour and as close together as possible. In no instance was the A horizon less than 6 in. in depth.

Moisture equivalent, pH, and total nitrogen were determined on all samples; per cent. silt and clay on the 0–1 in., 4–5 in., and 5–6 in. samples; and organic carbon was determined on the 0–1 in. samples. The determinations of moisture equivalent, pH, organic carbon, and per cent. silt and clay were according to Piper (1942), the combustion method being used for organic carbon, and the hydrometer

method for per cent. silt and clay. Total nitrogen was determined by the Kjeldahl method.

A statistical analysis of the data left some doubt as to the significance of the results obtained. The test using the variation between locations within sites as error corresponds to testing the individual mean differences with this pooled error, determining the probabilities, and then combining these probabilities through the mean of equivalent t variates with the same error variance. This procedure could give a significant probability if one of the sites gave rise to an extremely significant difference while others gave either no difference or even reversed the sign. On the other hand, it is fairly certain that with a real effect one would expect it to be of varying magnitude but consistent in sign between sites, so that the interaction variance of species with sites will tend to be excessive in appraising whether there is evidence of consistent real effects but possibly differing in degree.

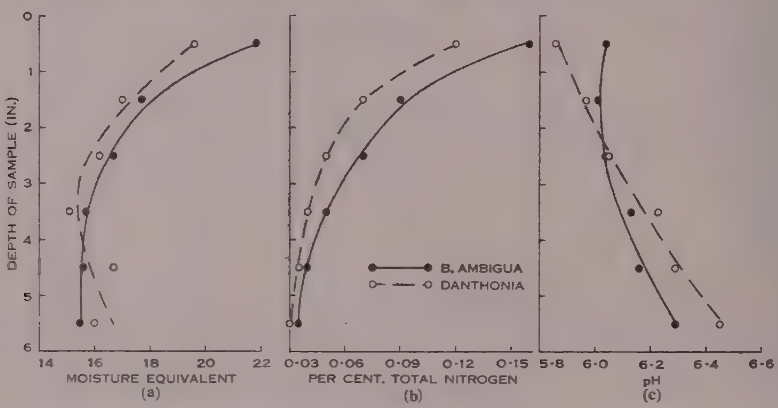

Fig. 1.—Changes in moisture equivalent, total nitrogen, and pH with depth in soils from *B. ambigua*- and *Danthonia*-dominant areas.

A confirmatory study was made of the total nitrogen and pH contrasts in the 0–1 in. zone by taking six paired locations within each of six sites. (Sites *A*, *B*, and *C*, and three new sites, *D*, *E*, and *F* were sampled in October 1955 for this purpose). The contrast of species using the species × sites interaction as error was in each instance significant at the 1 per cent. level at least. This lends confidence that the use of the variance between locations within sites as a measure of error for the existence of real effects is satisfactory.

IV. Results

Figure 1 summarizes the results for moisture equivalent, pH, and total nitrogen, the graphs being drawn from the mean figures for all samples at the initial sampling. The moisture equivalent of the soils under *B. ambigua* appears to be higher for the first 3 in. than for the soils under *Danthonia*, but a significant difference can be established only at 0–1 in. (Fig. 1(*a*)). Soil pH is significantly higher under *B. ambigua* at 0–1 in., while at 3–4 in. and 5–6 in. it is significantly lower than under

Danthonia (Fig. 1(*c*)). The nitrogen content of the soils under *B. ambigua* is significantly higher than under *Danthonia* (Fig. 1(*b*)) at all depths except 4–5 in.

Table 1 shows the mean values for the percentage of silt and clay at sites *A*, *B*, and *C* for the 0–1 in., 4–5 in., and 5–6 in. samples. Significant differences

Table 1

MEAN VALUES FOR PERCENTAGE SILT + CLAY IN SOILS UNDER B. AMBIGUA AND DANTHONIA

Site	0–1 in.		4–5 in.		5–6 in.	
	B. ambigua	*Danthonia*	*B. ambigua*	*Danthonia*	*B. ambigua*	*Danthonia*
A	45·3	41·9	47·4	44·5	39·5	35·8
B	37·4	38·1	36·1	39·6	43·7	44·0
C	35·9	32·4	38·1	42·0	40·5	43·7
General Mean	39·5*	37·5*	40·5	42·0	41·2	41·2

* $P < 0{\cdot}05$.

were demonstrated only in the 0–1 in. samples, where the percentage of silt and clay in the soils under *B. ambigua* is higher than that of the soils under *Danthonia*.

Table 2

MEAN VALUES FOR TOTAL NITROGEN AND pH FOR 0–1 IN. SAMPLES AT SIX SITES COLLECTED OCTOBER 1955

Site	Total N (%)		pH	
	B. ambigua	*Danthonia*	*B. ambigua*	*Danthonia*
A	0·16	0·125	6·06	5·96
B	0·18	0·17	5·74	5·59
C	0·26	0·235	6·04	5·90
D	0·14	0·10	6·10	5·89
E	0·22	0·19	6·01	5·60
F	0·19	0·16	6·11	5·97
General Mean	0·19	0·16	6·01	5·82

Table 2 shows the mean values for total nitrogen and pH in the 0–1 in. samples collected from six sites in October 1955. Both total nitrogen and pH are significantly higher under *B. ambigua* than under *Danthonia*. (See note on statistical analysis in Section III.)

V. Discussion

An examination of Figure 1(a) indicates that in the A horizon moisture equivalent decreases with depth. It would therefore appear that on more or less

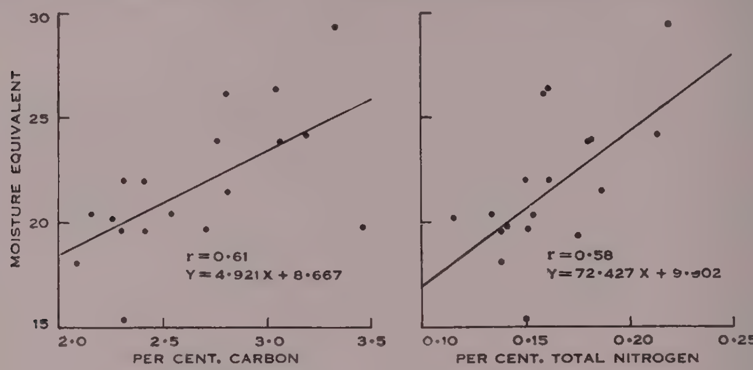

Fig. 2.—Regression of moisture equivalent on per cent. organic carbon and per cent. total nitrogen for 0–1 in. samples under *B. ambigua.*

eroded areas the moisture equivalent at the new soil surface would be less than that at the original surface, and that after the establishment of *B. ambigua* the moisture equivalent increases to a point greater than that of the original surface soil.

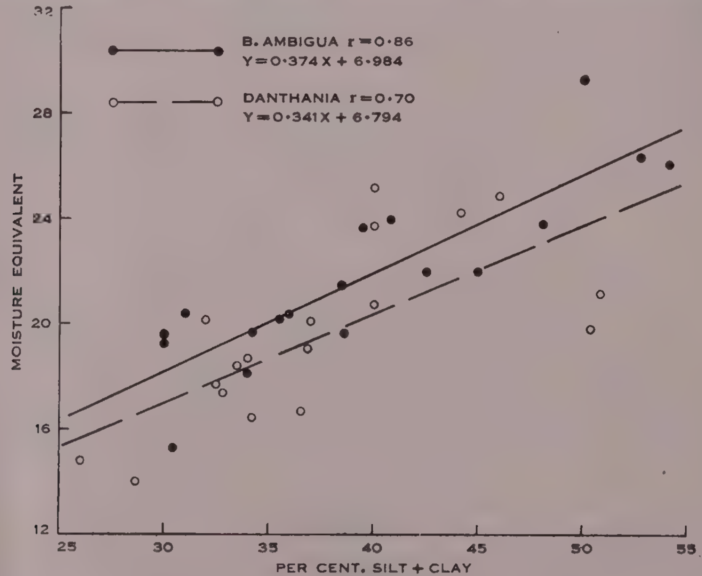

Fig. 3.—Regressions of moisture equivalent on per cent. silt + clay for 0–1 in. samples under *B. ambigua* and *Danthonia.*

The regressions of moisture equivalent on per cent. carbon and per cent. nitrogen are shown in Figure 2 for the 0–1 in. samples under *B. ambigua.* It is

clear that a significant correlation exists. No correlation between moisture equivalent and per cent. nitrogen or carbon could be demonstrated for the 0–1 in. samples under *Danthonia*. It therefore appears probable that the moisture equivalent of the 0–1 in. samples under *B. ambigua* is, to some extent at least, influenced by the organic matter.

The soils examined contain a high percentage of silt, which has a marked effect on moisture equivalent. It was found that there is a closer correlation between moisture equivalent and per cent. silt + clay than either of these fractions considered separately.

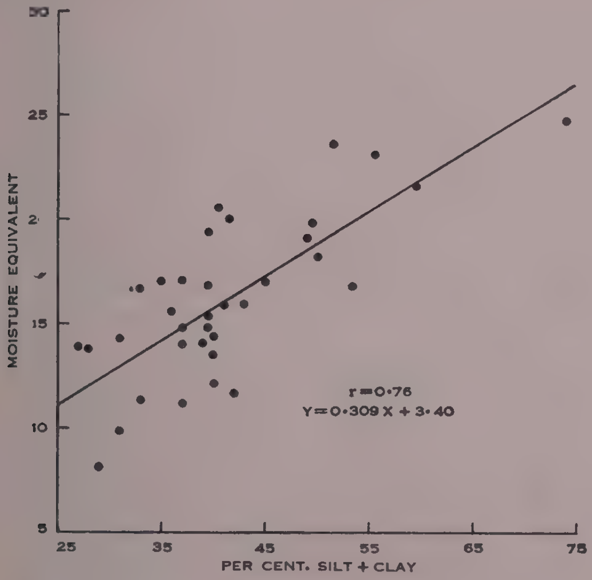

Fig. 4.—Regression of moisture equivalent on per cent. silt + clay for 4–5 in. samples from both *B. ambigua* and *Danthonia* communities.

The regressions of moisture equivalent on per cent. silt + clay for the 0–1 in. samples under *B. ambigua* and *Danthonia* are shown in Figure 3. It appears that some factor affecting moisture equivalent other than per cent. silt + clay may differ in the two sets of samples. Figures 4 and 5 show the regression of moisture equivalent on per cent. silt + clay for the 4–5 in. and 5–6 in. samples respectively. Here a common regression for both species has been calculated, as there is no real difference between the curves for the separate species. At these depths the organic matter content of the soils under both species is less than that of the 0–1 in. samples under *Danthonia*. This further supports the suggestion that organic matter is influencing the moisture equivalent of the soils under *B. ambigua* at 0–1 in.

At 0–1 in. the differences in moisture equivalent at common per cent. silt + clay for the two species does not reach significance at 5 per cent. ($P = 0 \cdot 077$), but since there are clear indications of an effect of organic matter on moisture

equivalent under *B. ambigua* (see Fig. 2), it is postulated that the higher values under this species are in part due to the higher organic matter content, though they are chiefly a reflection of a greater percentage of silt + clay.

If it is true that *B. ambigua* initially establishes in areas where the moisture equivalent of the soil is lower than that in those areas where *Danthonia* spp. are dominant, the increase in the percentage of silt and clay at the surface must follow its establishment. It has been observed that *B. ambigua* is relatively unpalatable

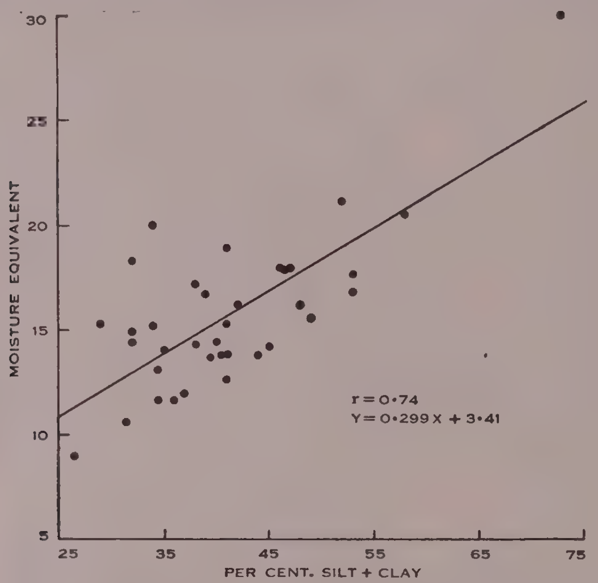

Fig. 5.—Regression of moisture equivalent on per cent. silt + clay for 5–6 in. samples from both *B. ambigua* and *Danthonia* communities.

to sheep, and that it is seldom heavily grazed. In contrast, *Danthonia* spp. may be heavily grazed, especially during periods of low production. These species are thereby weakened, and erosion of the surface soil is accentuated. It is suggested that the increase in the percentage of silt and clay in the surface under *B. ambigua* results from accumulation of the finer particles washed from higher levels where the *Danthonia* sward has been weakened.

It has been observed that *B. ambigua* frequently establishes where the percentage of the finer soil particles is higher than in neighbouring *Danthonia*-dominant areas. These include roadsides where the B horizon may be exposed, and places where silt and clay are deposited after being washed from higher levels. (No such sites were sampled for the present study.) In the general case studied, the evidence suggests that the moisture equivalent and per cent. silt and clay at the surface were initially lower in areas invaded by *B. ambigua* than in neighbouring *Danthonia* areas. In the two special cases of establishment of *B. ambigua* on exposed B horizon and on deposits washed from higher levels, the position is reversed. It would there-

fore appear that soil texture is not a limiting factor in the establishment of *B. ambigua*.

There is no indication in the majority of stands of *B. ambigua* that deposition of silt and clay or exposure of the B horizon occurred prior to invasion and, from the evidence presented, it is concluded that, in general, increases in moisture equivalent and per cent. silt + clay occur after invasion.

The increase in organic matter under *B. ambigua* is chiefly a direct result of its unpalatability, the bulk of the plant litter being deposited *in situ* instead of being removed by the grazing animal, as occurs with the more palatable species such as *Danthonia*. (Sheep grazing on natural pastures deposit a large proportion of the organic matter as faeces and urine at stock camps, usually under trees, or at or near the tops of hills.) The greater quantity of dead and decomposing litter from *B. ambigua* as compared with *Danthonia* can readily be seen in the field. No doubt some organic matter washed from higher levels also accumulates in stands of *B. ambigua*.

The changes in soil pH with depth following establishment of *B. ambigua* are probably due to the greater capacity of this species to absorb cations from the lower depths. This would result in a decrease in soil pH such as has been demonstrated below 3 in. The increase in pH at the surface is then presumably due to the deposition of the cations in the plant litter, and their subsequent release on its decomposition.

VI. Acknowledgments

The author is indebted to Mr. G. A. McIntyre, Division of Mathematical Statistics, C.S.I.R.O., for the statistical examination of the data; to the General Chemistry Section, Division of Plant Industry, C.S.I.R.O., for determination of total nitrogen and organic carbon; and to Miss S. Angell and Mr. W. A. Bruce for assistance in the determination of moisture equivalent, pH, and per cent. silt and clay.

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DARK ISLAND HEATH (NINETY-MILE PLAIN, SOUTH AUSTRALIA)

I. DEFINITION OF THE ECOSYSTEM

By R. L. Specht* and Patricia Rayson*

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Summary

A survey of the literature on the distribution of the sclerophyllous understorey in Australia leads to the conclusion that, although the climatic conditions under which it grows may vary considerably, the soils on which it flourishes are always acid and very low in available phosphorus and nitrogen and sometimes in potassium, copper, zinc, and molybdenum. The problem is how the sclerophyllous species are able to flourish on such deficient soils.

To provide a background for the investigation of this problem, a detailed ecological study was initiated on an extensive stand of heath occurring on deep sand (the Makin sand) in the upper south-east of South Australia. This paper outlines the habitat and indicates the general characteristics of the heath vegetation of the area.

The climate is typical of a mediterranean region; the soil is a deep, acid sand, remarkably low in most mineral nutrients; the vegetation is scarcely influenced by grazing animals, but is regularly razed by fire.

The vegetation is dominated by a number of nanophanerophytes, not more than 6 ft in height, with an understorey of chamaephytes, hemicryptophytes, and geophytes. The majority of the species possess dull green, small, sclerophyllous leaves (leptophylls). Growth occurs predominantly during the summer, from January to March, while many of the species flower during spring. Most of the dominant species, however, flower during late summer to midwinter. Leaf-fall is greatest towards the end of the dry summer period, while litter decomposition, which is only completed after $1\frac{1}{2}$–$2\frac{1}{2}$ years, reaches its maximum in the spring.

It is shown that it is necessary to examine at least four random quadrats of at least 25 sq. yd to study satisfactorily the larger species. In each quadrat, a smaller random sub-quadrat of at least 22 sq. ft will enable the critical examination of the smaller species.

The outstanding features of the southern Australian heath are (1) a summer-growth rhythm instead of the spring growth typical of similar vegetation in other mediterranean-type regions, and (2) its consistent occurrence on soils very low in fertility. It is suggested that these are connected with the evolutionary history of the heath which apparently flourished during the Pliocene period on widespread, infertile, lateritic podsols in equilibrium with a warm pluvial climate favouring summer growth.

I. Introduction

Andrews (1916), Prescott (1931), and Wood (1950) have indicated the widespread occurrence of a typically Australian element in the vegetation of Australia. Sclerophyllous shrubs, belonging chiefly to the Australian sections of the families Leguminosae, Proteaceae, Epacridaceae, Rutaceae, and Casuarinaceae,† occur in

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† Nomenclature as in Black (1943–57) unless stated otherwise (see Appendix I). The cryptogamic flora is listed in Appendix II.

dense assemblages in the higher-rainfall regions of Western Australia, South Australia, Tasmania, Victoria, and New South Wales, and extend in small pockets along the coast of Queensland as far north as Bundaberg (Coaldrake, personal communication). In some areas this assemblage of sclerophyllous shrubs may occur alone in a heath formation; in other areas it is found as the understorey to mallee in a mallee-heath formation, to woodland trees in a dry sclerophyll woodland formation, or to forest trees in dry to wet sclerophyll forest formations.

Casual examination of any of these formations, wherever they occur in Australia, shows that the physiognomy of the understorey and the species themselves appear similar. Actually many of the genera present are the same, but, as Wood (1937, 1950) has shown, the species present within these genera are often closely allied vicarious species.

As one would expect from the occurrence of this sclerophyllous understorey in such a large range of communities, the climate—and consequently those properties of the soil closely dependent upon climate—vary greatly. The length of the growing period, based upon the climatic index $P/s.d.^{0 \cdot 75}$ (Prescott and Thomas 1948–49), varies from 6–7 months to 12 months of the year with the value of the index exceeding 4; 4–9 months of that growing period will have an index greater than 8. Even under identical climatic conditions factors such as soil moisture may vary greatly because of variations in run-off, soil texture, and impeded drainage, and yet the sclerophyllous understorey is continuous with little change in the composition of the major species (e.g. Crocker 1944).

The soils are consistently very low in major elements for plant growth (e.g. phosphorus, nitrogen, and potassium) and may be low in the microelements copper, zinc, and molybdenum. The surface soil and usually the subsoil are acid to neutral. The soils are strongly podsolized under higher-rainfall conditions and become progressively less podsolized as the rainfall deteriorates, until, in the drier limit of the vegetation, solonization is the main factor inducing leaching of the finer particles and nutrients within the soil; however, at this limit the parent material also plays a large part in the fertility of the soil. In the climatic zone with a growing period of 6–7 months of the year, soils derived from siliceous rocks, residual lateritic podsols, and lateritic sandplains are low in fertility and support a sclerophyllous understorey, whereas soils derived from argillaceous rocks are higher in fertility and support a savannah woodland formation. Boundaries, often less than a chain in width, may be seen frequently between the sclerophyllous understorey developed on the infertile soil and the herbaceous understorey on the more fertile soil (e.g. Pidgeon 1937; Crocker 1944; Specht and Perry 1948; Specht 1951; Beadle 1954). The distribution of these and several other plant communities led Wood (1939) to stress the edaphic factor in the classification of plant communities. In that paper, he illustrated the importance of phosphorus, nitrogen, and pH levels of the soil in governing the limits of eight plant communities of South Australia. The same conclusions have been drawn by Beadle (1953, 1954) for the vegetation of eastern Australia, where he confirmed Wood's data on phosphorus by both chemical and biological tests for the fertility of the soils. Beadle's data (1954) indicated that phosphorus is undoubtedly the major limiting element, but that once this is supplied as fertilizer, nitrogen often becomes

TABLE 1

CLIMATIC AND SOIL CHARACTERISTICS WHICH CONTROL THE DISTRIBUTION OF THE SCLEROPHYLLOUS UNDERSTOREY IN AUSTRALIA

Locality	Formation	No. Months with $P/s.d.^{0\cdot75}>4$	Soil	Soil N (%)	Soil P_2O_5 (%)	Soil pH	References	Recorded Deficiencies	References to Deficiency Data
South-West Western Aust.	Sclerophyll forest		Podsols and residual podsols	0·011–0·281	0·004 0·007	4·5 6·5	Williams (1931–32) Gardner (1941–42) Prescott (1944) Smith (1951*a*, 1951*b*) Speck (1952)	P, N, K, Cu, and Zn	Mursell (1944) Jones and Elliott (1944) Rossiter and Kipps (1947) Rossiter (1947, 1951)
	Heath	7–10	(1) Coastal dunes (2) Wet acid soils	(1) Low (2) 0·035	(1) Low (2) Low	(1) 8·2–9·3 (2) 4·9–6·7			
	Mallee-heath and heath	5–7	Solonized soils	Low	Low	6·8–8·6			
Eyre Pen., South Aust.	Sclerophyll woodland and heath	7	Podsolic soils	Low	Low	Acid	Crocker (1946*b*)	P and N	
Mt. Lofty Ranges, South Aust.	Sclerophyll forest	9–11	Podsols, residual podsols, and skeletal quartzites	0·019–0·090	0·003–0·008	5·1–6·7	Specht and Perry (1948)	P, N, and Mo	Anderson, Thomas, and Oertel (1946)
Kangaroo I., South Aust.	Sclerophyll forest Sclerophyll. scrub	7 8	Residual podsols and sands	0·033–0·083	0·002–0·021	5·0–6·5	Baldwin and Crocker (1941) Northcote and Tucker (1948)	P, N, Cu, and Mo	Northcote and Tucker (1948)
Lower South-East, South Aust.	(1) Sclerophyll forest (2) Heath	8–10	(1) Podsolized sands (2) Clay posdols	<0·1 <0·1	<0·01 0·003–0·005	4·7–6·6	Stephens *et al.* (1941) Crocker (1944) Blackburn (1952)	P, N, Cu, and Zn	Crocker and Tiver (1946) Tiver and Crocker (1951)
Upper south-east, South Aust.	Mallee-heath and heath	7–8	Solonized soils	0·003–0·013	0·001–0·020	5·8–7·9	Taylor (1933) Jessup (1946) Specht (1951) Coaldrake (1951)	P, N, Cu, and Zn	Riceman (1948, 1949, 1950) Anderson and Neal-Smith (1951)
Victoria	Sclerophyll forest Heath	9–12	Podsolic soils	Low	Low	4·8–5·9	Prescott (1931, 1944) Leeper (1948) Patton (1933)	P and N	Leeper (1948)

TABLE 1 (*Continued*)

Locality	Formation	No. Months with $P/s.d.^{0.75} > 4$	Soil	Soil N (%)	Soil P_2O_5 (%)	Soil pH	References	Recorded Deficiencies	References to Deficiency Data
Tasmania	(1) Sclerophyll forest (2) Heath	9–12	(1) Normal podsols (2) Humus podsols	0·05–0·50 0·02–0·46	0·01–0·09 0·002–0·02	4·1–6·9 4·0–6·5	Stephens (1941)	P, N, and B	Stephens (1941)
Coastal New South Wales	Sclerophyll forest Sclerophyll woodland Heath	9–12	Residual podsols, podsolic soils, and skeletal sandstone	0·079–0·147	0·036–0·137	Acid	Pidgeon (1937) Beadle (1954)	P and N (?)	Beadle (1954)
Aust. Capital Territory	Sclerophyll forest	9–12	Podsolic soils	Low	Low	Acid	Pryor (1938)	P and N	
Coastal Queensland	Wallum and heath	9–12	Low-lying deep sands	Low	Very low	Acid	Coaldrake (personal comm.)	P, K, N, Ca, Cu, Zn, Mo, and B	Andrew and Bryan (1955)

limiting. These results have been confirmed by many agronomists (see Table 1) and by the authors.

Wherever this sclerophyllous understorey occurs in Australia, the climate is usually suitable for the growth of many pasture and crop species, but in all cases the marked deficiencies of phosphorus and nitrogen and sometimes of minor elements,

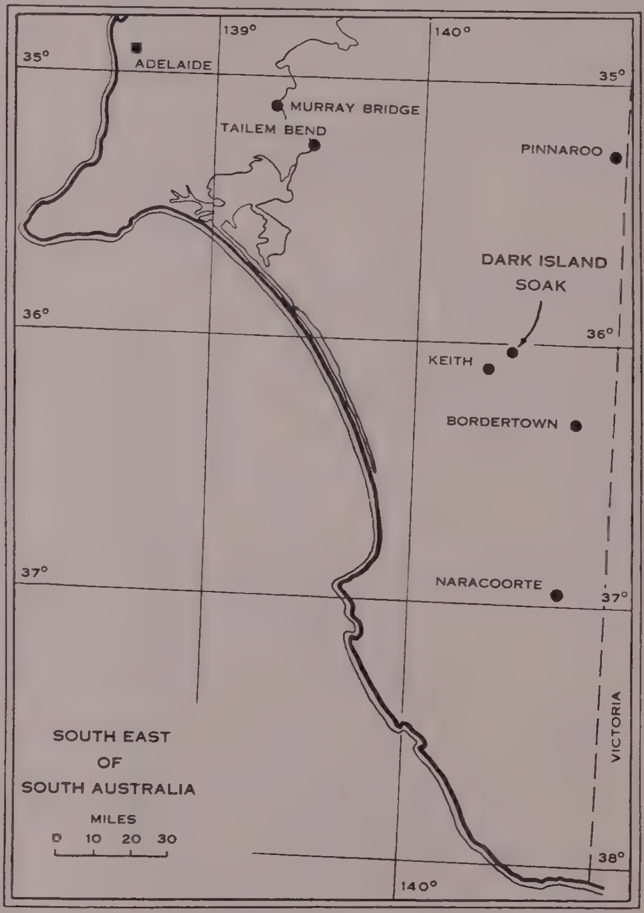

Fig. 1.—Map showing the location of Dark Island Soak in the upper south-east of South Australia.

copper, zinc, and molybdenum, must be corrected to allow optimum growth of species of agricultural value. The problem arises of why sclerophyllous species flourish on such deficient soils, whilst agricultural species fail.

Before it is possible to investigate satisfactorily these problems it is necessary to obtain detailed ecological data concerning at least one sclerophyllous understorey. For this purpose, a relatively uniform area was chosen near the centre of a considerable stand of heath in the upper south-east of South Australia and located 10 miles north-

east of Keith, near Dark Island Soak (Fig. 1). The heath grows on undulating sand 5–80 ft deep, which is relatively uniform in composition throughout much of its depth (Coaldrake 1951; Blackburn *et al.* 1953).

Studies on the complete ecosystem (Tansley 1935; Lindeman 1942; Crocker 1952) of this area are in progress.

II. The Climate

The general characteristics of the climate of the area under consideration have been discussed by Coaldrake (1951).

The nearest meteorological station to the experimental area is at Keith, 9 miles to the south-west. Rainfall data collected at Waljena homestead, 2 miles to the east of the experimental area, are almost identical with those at Keith (Coaldrake 1951). One can assume, therefore, that the experimental area has a climate approximately the same as that at Keith.

Rainfall records have been kept at Keith for 43 years, but temperature records have been available for only 6 years. These records are summarized in Table 2.

(*a*) *Rainfall and Evaporation*

Typical of a mediterranean region, the climate shows marked seasonal alternation of hot, dry summers with cool, wet winters. The area receives approximately 18 in. of rainfall per annum, 70–75 per cent. of which falls during the months May to November. This is the period of influential rainfall during which the surface 4 in. of soil are maintained above the wilting point (Trumble 1937). Trumble (1948) has estimated that, on the average, the area is subject to drought years—i.e. years with less than five consecutive months of influential rainfall—once in every five years.

Mean annual evaporation from a free water surface greatly exceeds mean annual rainfall, and evaporation is less than rainfall for four winter months only.

(*b*). *Growing Season*

The effect of seasons of high evaporation and low rainfall alternating with seasons of low evaporation and high rainfall is adequately shown by the Prescott index (Prescott and Thomas 1948–49; Prescott 1949–50); Prescott, Collins, and Shirpurkar 1952), which indicates that, on the average, Keith experiences:

7·1 months of the year with $P/E^{0\cdot75}>0\cdot4$
4·9 months of the year with $P/E^{0\cdot75}>0\cdot8$
3·8 months of the year with $P/E^{0\cdot75}>1\cdot2$
2·8 months of the year with $P/E^{0\cdot75}>1\cdot6$
1·4 months of the year with $P/E^{0\cdot75}>2\cdot0$

These data indicate that agriculture is reasonably secure within the area. The period of influential rainfall of 7·1 months includes a period of 4·9 months during which adequate water is available for vegetation of low transpiration rates (Specht 1953). Within this period, soil becomes saturated with water for 3·8 months of the year when run-off or internal drainage occurs, the amount increasing in intensity towards the middle of winter (June–July).

TABLE 2

MEAN CLIMATIC DATA FOR KEITH

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Year
Temperature													
Maximum (°F)	87	82	81	70	65	59	59	60	67	70	75	82	70
Minimum (°F)	54	52	51	46	45	42	40	41	43	46	48	51	49
Mean (°F)	70	67	66	58	55	50	49	50	55	58	61	67	59
Terrestrial minimum (°F)	48	46	45	39	39	36	33	34	37	41	43	45	41
Rainfall (in.)	0·66	0·96	0·84	1·28	2·08	2·01	2·12	2·12	2·06	1·60	1·26	1·00	17·99
Days of rain	4	4	4	7	11	12	14	14	12	10	7	5	104
Saturation deficit	0·476	0·311	0·288	0·165	0·068	0·047	0·047	0·073	0·155	0·207	0·294	0·410	
Evaporation ($E_w = 21$ *s.d.*) (in.)	10·00	6·54	6·05	3·47	1·43	0·99	0·99	1·53	3·26	4·35	6·18	8·62	53·41
Prescott ratio—$P/E_w^{0·75}$	0·12	0·23	0·22	0·50	1·59	2·03	2·14	1·53	0·85	0·53	0·32	0·20	
Potential evaporation (Prescott—8 $(s.d.)^{0·75}$)	4·58	3·33	3·14	2·07	1·07	0·81	0·81	1·12	1·97	2·46	3·19	4·09	28·64
Potential evapotranspiration (Thornthwaite) (in.)	4·95	3·33	3·48	1·92	1·56	0·98	0·98	1·18	1·72	2·68	3·08	4·50	30·36
Storage change (in.)	0	0	0	0	0·52	1·03	1·14	0·94	0·34	−1·08	−1·82	−1·07	
Storage (in.)	0	0	0	0	0·52	1·55	2·69	3·63	3·97	2·89	1·07	0	
Actual evapotranspiration (in.)	0·66	0·96	0·84	1·28	1·56	0·98	0·98	1·18	1·72	2·68	3·08	2·07	17·99
Water deficiency (in.)	4·29	2·37	2·64	0·64	0	0	0	0	0	0	0	2·43	12·37
Water surplus (in.)	0	0	0	0	0	0	0	0	0	0	0	0	0
Moisture ratio $\left(\frac{p-e}{e} = \frac{p}{e} - 1\right)$	−0·83	−0·71	−0·76	−0·67	0·13	1·06	1·16	0·80	0·20	−0·40	−0·59	−0·78	

If the potential evapotranspiration of Thornthwaite (1948) or the potential evaporation of Prescott, Collins, and Shirpurkar (1952) is calculated from the data, each is found to be approximately equal. From the monthly figures for potential evapotranspiration and rainfall, it is possible to estimate the water storage change, water storage in the soil, the actual evapotranspiration, and the water deficiency or surplus for each month. These results are included in Table 2 and Figure 2. It will

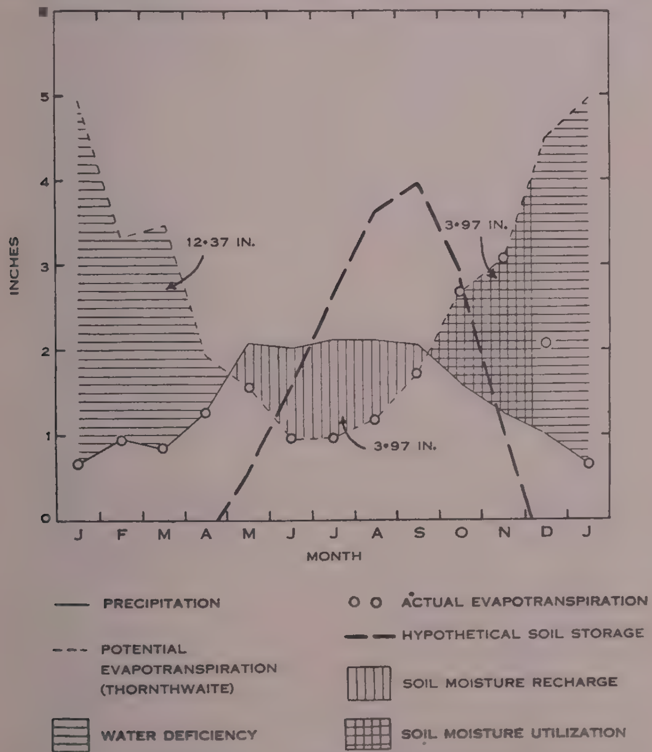

Fig. 2.—Graphs showing the monthly rainfall, the potential evapotranspiration and the hypothetical soil moisture storage at Keith, South Australia.

be seen that the growing season of annual plants indicated above as 7·1 months may be extended into early December by the utilization of soil moisture stored from the winter season. Even this estimate is too small compared with observations in the field (Specht 1953), which showed that the soil moisture lasts well into January.

The climate would be classified by Thornthwaite (1948) as a semi-arid, mesothermal (of the second order) climate, which has little if any seasonal water surplus: viz. $DB'_2\ d\ a'$.

(c) *Air and Soil Temperatures*

Data for air temperatures are summarized in Table 2. From these it would be expected that growth would be limited during midwinter.

The daily fluctuations in air temperature are paralleled by fluctuations in the soil temperatures. Temperature readings at depths of 3, 6, and 12 in. were made in open areas at hourly intervals from 7 a.m. to 6 p.m. at approximately monthly intervals throughout the year. Figure 3 shows the fluctuation in soil and air tempera-

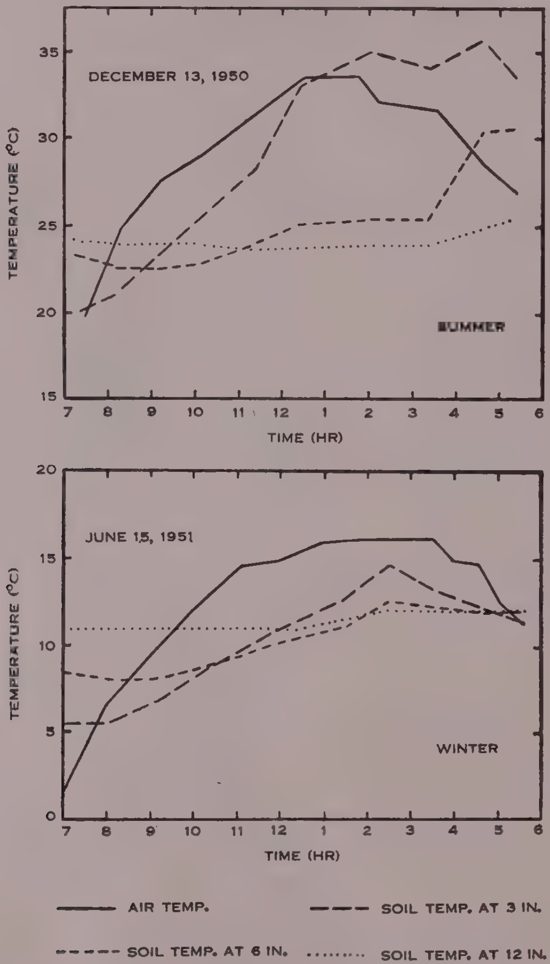

Fig. 3.—Graphs showing the hourly changes in soil temperature at depths of 3, 6, and 12 in. under the heath vegetation near Dark Island Soak during a summer and a winter day.

tures throughout a day during midsummer and midwinter. There is a marked decrease and lag in the daily changes in temperature as soil depth increases. Fluctuations at a depth of 12 in. become insignificant in comparison with those at higher levels. Figure 4 shows the maximum and minimum soil temperatures observed during each set of observations. The soil temperature at 3 in. fluctuates between the winter and

summer extremes of 1·9 and 45·0°C; at 6 in. between 4·1 and 36·0°C; and at 12 in. between 5·8 and 29·0°C. These fluctuations will be of even greater magnitude in the surface layer of the soil, for the temperature gradient with depth is very steep, e.g. the following soil temperatures were recorded at 1.00 p.m. on September 8, 1951, at

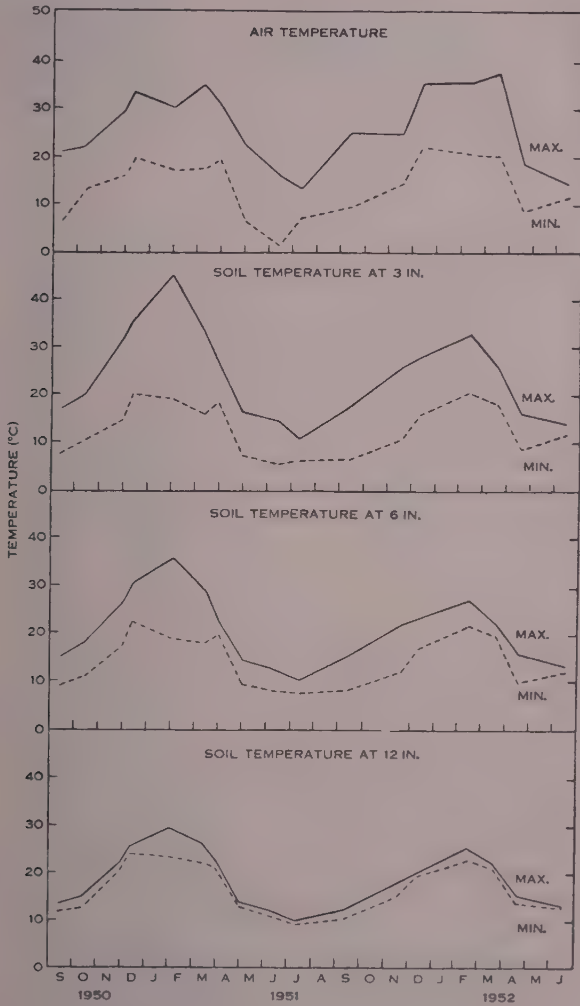

Fig. 4.—Graphs showing changes in soil temperature at depths of 3, 6, and 12 in. under the heath vegetation near Dark Island Soak throughout the years 1950–52.

the depths stated, at a time when the air temperature was 23·4°C. Surface, 22·0°C; ½ in., 18·1°C; 1 in., 17·2°C; 2 in., 16·1°C; 3 in., 14·7°C; 4 in., 13·8°C; 5 in., 13·1°C; 6 in., 12·2°C. There is a gradual decrease in temperature with depth during the summer months, whereas an increase occurs during the winter months. However, as

shown in Figure 5, the seasonal fluctuations decrease with increasing depth; the 12-in. depth shows variations from 9·5 to 24·0°C, whereas the 60-in. depth shows variations from 12·0 to 20·7°C.

Superimposed upon the daily and seasonal variations is the effect of the shading of the larger shrubs such as *Banksia ornata*. Differences of up to 4·1°C have been observed during summer at a depth of 3 in. under shaded areas in contrast to exposed soil. These differences becomes less marked both with depth and during winter months.

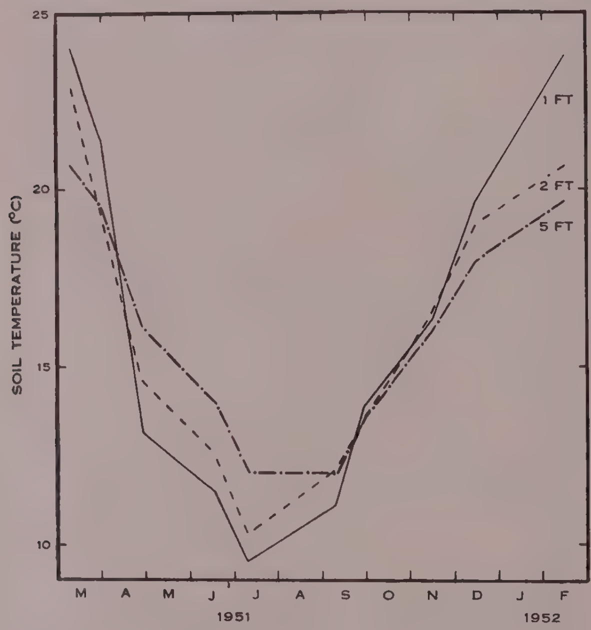

Fig. 5.—Graphs showing the monthly changes in soil temperature at depths of 1, 2, and 5 ft under the heath vegetation near Dark Island Soak during 1951–52.

It is apparent that a complex spatial and seasonal pattern of soil temperature is present within the Makin sand, and this will have significant effects on the activity of soil microorganisms as well as on higher plants.

(*d*) *Frosts and Dews*

In a recent survey of the climate of the Tatiara district, Mason (1952) states "It will be seen that frosts can be expected in every month of the year although from November to February they are not common. At Keith, which is probably typical of quite a large part of this area, the temperature gradient between the ground and the screen on frosty nights is steep, the difference between the terrestrial and screen minimum temperatures being commonly of the order of 10 degrees. The lowest temperature recorded on the grass was 18 degrees and in several months 10 degrees or more of frost was recorded by the terrestrial thermometer".

Dews are more frequent than frosts and they occur in every month throughout the year. No reliable records of their occurrence are available.

(e) *Winds*

Since the winds at Keith have been observed for only 5 years, the wind roses illustrated in Figure 6 show only trends in the wind system. At 9.00 a.m., southerly components are more prominent during summer months whereas northerly winds tend to be more prominent during winter. Winds blowing directly from the east are rare;

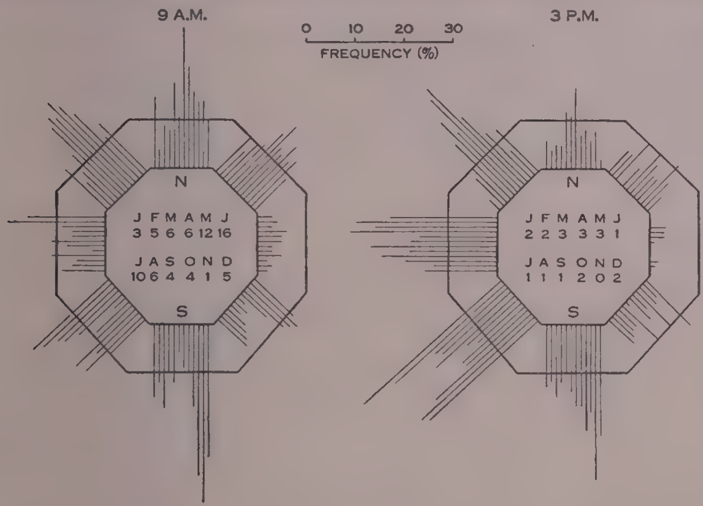

Fig. 6.—Wind roses for 9 a.m. and 3 p.m. indicating the frequency of occurrence of winds from each of the eight points of the compass. The outer octogen indicates the 10 per cent. frequency level. The percentage of calm days are indicated within the roses for each month of the year.

west winds, although not inconsiderable throughout the year, tend to become more important during November–December. The 3 p.m. records indicate a marked swing of the winds from the north-east and north towards westerly directions. East winds are a rarity in the afternoon.

Although a high proportion of calms are recorded at 9 a.m., wind generally rises in the afternoon especially during the winter months. Winter rain-bearing winds usually blow from a westerly direction, but the freak monsoonal rain-storms occurring in summer may strike from almost any direction.

III. The Soil and the Topography

Coaldrake (1951) indicated the polygenetic origin of the soils of the Buckingham suite of the Ninety-Mile Plain from deep. alluvial soils of the old River Murray delta which were superimposed by desert sands during the Arid period (Crocker 1946*a*). He showed how the variable depth of sand, which is typical of former desert conditions, influenced distribution of the major vegetation communities. Heath vegetation

dominates areas where depth of sand is 4 ft or more; Coaldrake described this deep sand as the Makin sand. More recently, Blackburn *et al.* (1953), in their soil survey of the area, referred to it under the heading "Soils of Broken Sandhill Areas".

The experimental area near Dark Island Soak is a gently undulating sandplain dissected at intervals by high seif (especially to the west of the area) and barchan-like dunes, both of which have their major axis running approximately north to south. The easterly slip faces of these dunes are steep in comparison with the westerly approach.

Table 3

SOIL DATA FOR THE MAKIN SAND

	A_1	A_2	A_3	B	Technique
Depth	0 to 10 in.	10 to X in.	X to (X+6) in.	Deeper than (X+6) in.	
Mech. analysis					
Coarse sand (%)	5·4	3·5	5·9	13·2	Hydrometer Method (Piper 1944)
Fine sand (%)	92·7	94·4	92·8	21·8	
Silt (%)	0·8	0·2	0·0	1·5	
Clay (%)	1·1	1·9	1·3	63·5	
pH	5·76	6·40	6·40	6·26	Raupach (1951*a*, 1951*b*)
Phosphorus (p.p.m.)	8	7	6	55	J. Hutton (unpubl. data)
Nitrogen (%)	0·020	0·005	0·002	0·021	Piper (1944)
Copper (p.p.m.)	1·1	1·1	0·3	0·6	Jones (1952)
Zinc (p.p.m.)	1·55	1·56	0·90	12·5	Jones (1952)
Manganese (p.p.m.)	7·2	5·2	10·8	17·2	Piper (1944)
Carbon (%)	0·1–0·8	0·05	0·01	0·04	Piper (1944)

A thin layer of undecomposed litter is found under many bushes, but it never constitutes a continuous layer over the soil surface. The deep sands all show a grey surface zone to a depth of 6–10 in., where organic matter has accumulated. Below this is an A_2 horizon of yellow sand containing very little organic matter, and varying in depth with the total depth of sand over clay. The A_2 horizon grades into an A_3 horizon consisting of a white sand occasionally flecked with reddish mottlings. This A_3 horizon occurs in the 6–12 in. immediately overlying the B horizon; small quantities of pisolitic gravel up to $\frac{1}{2}$ in. in diameter are found in this horizon.

The surface of the B horizon is relatively horizontal and is quite independent of the overlying sand dunes and sandplains. It is composed of a solonized clay—or sandy clay for the first 6 in.—with irregularly domed columns. The colour of this horizon is usually grey at first but soon becomes reddish yellow with intense red mottlings.

Detailed mechanical and chemical analyses of the horizons of the Makin sand are given by Coaldrake (1951). Analyses for the experimental area are given in Table 3.

The A horizons, which contain mainly sand, are sharply differentiated from the B horizon of clay. The reaction is acid throughout, but slightly more acid in the A_1 horizon. Variations of up to one pH unit have been noted in samples taken at the same depth but a few feet apart.

The phosphorus content in the sandy A horizons is exceedingly low, but rises sharply in the B horizon to a level which is still very low when compared with that of other soils. Immediately under decomposing litter, the top $\frac{1}{4}$ in. of soil may contain 14 p.p.m. of phosphorus (mean of 24 samples); at 3 in. the soil contains 9 p.p.m. Beyond this depth, the amounts are relatively constant and range from 6 to 8 p.p.m.

The picture for nitrogen is essentially similar, except that the amount in the clay is scarcely higher than that at 3 in. The amount of nitrogen immediately under decomposing litter averages 0·054 per cent. nitrogen (mean of 24 samples) and falls rapidly to 0·019 per cent. at the 3-in. depth. The nitrogen content may fall to 0·001 per cent. in the A_2 horizons, but all the figures vary markedly with the amount of organic matter present in each sample. The nitrogen content increases to 0·021 per cent. in the B horizon.

IV. Biotic Influences

Native animals, such as the kangaroo, emu, black cockatoo, and a few introduced rabbits, exert a minor grazing pressure on the vegetation. The most important biotic influence is that of man in periodically firing the vegetation. Fires lit either accidentally or intentionally raze the vegetation at irregular intervals, often as frequently as once every 5 years. In any area the irregular patterns of these fires afford a complex of stands of regenerating heath.

V. Vegetation

(a) *Life Form and Leaf Size*

The vegetation of the area is a characteristic heath formation as described by Wood (1950). One hundred and four angiosperms, most of which are sclerophyllous and perennial in nature, have been recorded (see Appendix I).

Twenty-four of the species are confined to certain aspects of the sand dunes, but most are continuous throughout the area. Seventy-six species grow in the uniform vegetation of the sand plains; 33 of these are low perennial shrubs (nanophanerophytes), usually not more than 2 ft high though a few (4 spp.) may grow to a height of 6 ft. Chamaephytes (10 spp.), hemicryptophytes (13 spp.), and geophytes (14 spp.) are of lesser importance, while therophytes (3 spp.) and succulents (1 sp.) are rare. The epiphytic species, though only 2 in number, are quite common throughout the area. *Eucalyptus baxteri*, a mesophanerophyte, is restricted to the leeward side of most steep sand dunes.

Of the 102 species examined, 56 were leptophylls with a leaf area of less than 25 sq. mm. Most of the other species possess leaves which fall either into Raunkiaer's leaf-size class of nanophyll (20 spp.), or into a category between a leptophyll and a nanophyll (18 spp.). Six species, of which *Banksia ornata* is the most important, may be classed as microphylls; only the leaves of *E. baxteri* and *Xanthorrhoea australis* approach the size of mesophylls.

(b) *Growth*

The more mesophytic dwarf elements of the vegetation, such as the Gramineae, Haloragaceae, Scrophulariaceae, Rubiaceae, Goodeniaceae, Stylidiaceae, and Compositae, have their flush of growth in the spring, while the geophytes in the

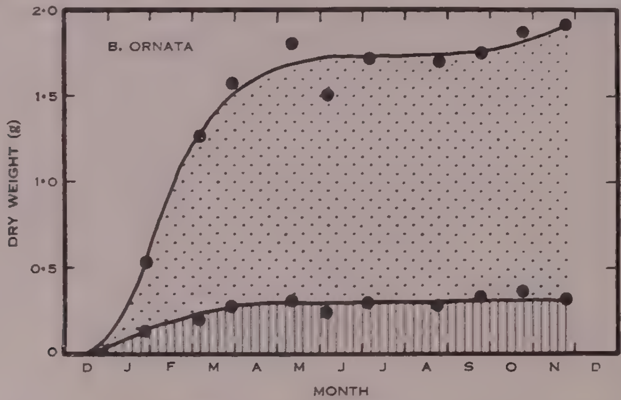

Fig. 7.—Dry weight of current terminal shoots of *Banksia ornata* at intervals throughout 1954. The dotted area represents the leaf material; the hatched area the stem.

families Orchidaceae, Liliaceae, and Droseraceae sprout, mature, and die during the winter and spring. The larger sclerophyllous species, which form the greater portion of the vegetation, show a period of maximum growth during summer, i.e. from

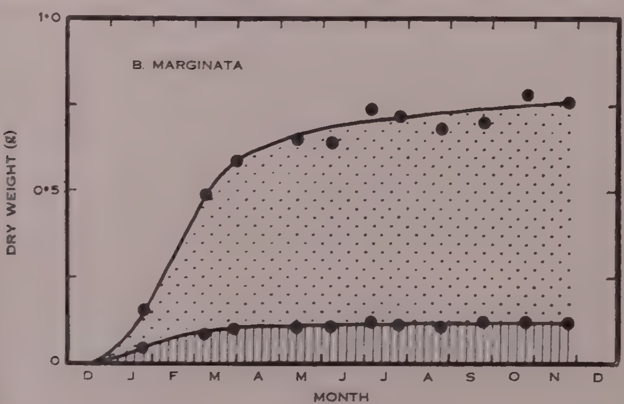

Fig. 8.—Dry weight of current terminal shoots of *Banksia marginata* at intervals throughout 1954. The dotted area represents the leaf material; the hatched area the stem.

mid December to March. The new shoots, then formed, gradually mature during the following colder months of the year. To illustrate this growth rhythm, five terminal shoots from each of 20 random specimens of both *B. ornata* and *Banksia marginata* were collected at monthly intervals during 1954. These shoots were dried to constant

weight, in an oven at 95°C, cooled in a desiccator, and weighed in sets of five. The stems were then stripped of leaves and reweighed. The results are graphed in Figures 7 and 8.

Growth appears to be initiated as soon as the mean air temperature rises above 65°F in December. Adequate soil moisture is usually available in the deep sands during December and January. Reserves may still be available in the B horizon clay during February and March, before the autumn rains fall in April. By autumn, however, the mean air temperature falls below 65°F and growth is inhibited.

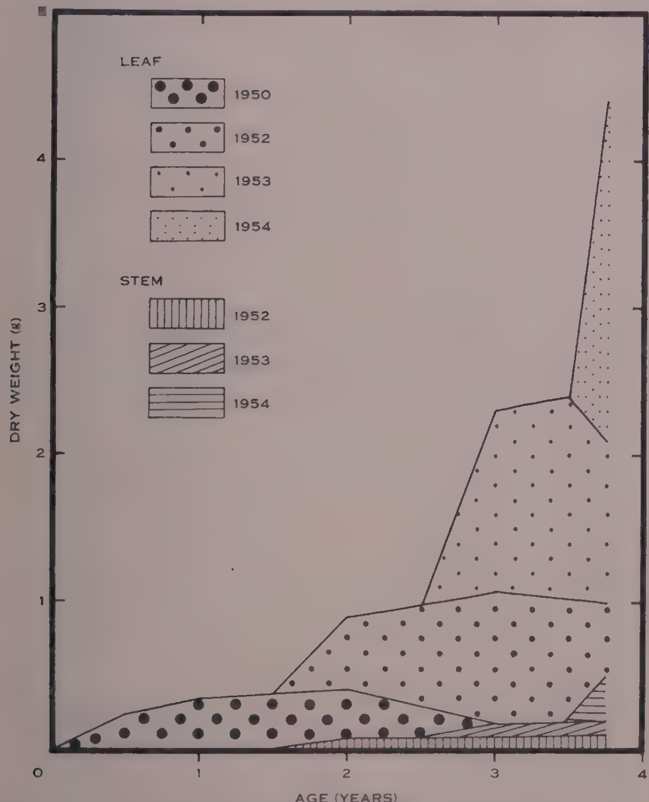

Fig. 9.—Dry weight of seedlings of *Banksia ornata* at intervals from June 1950, when the seeds germinated after a fire, until March 1954.

These observations contradict those of Patton (1933) who examined heath vegetation in Victoria and stated that "By November conditions have become fairly unfavourable for growth . . . Growth does not commence again until after the autumn rains. The rainfall is fairly evenly distributed over the year and, as a matter of fact, the six summer months, October to March, actually receive more rain than the six winter months, April to September". Our observations suggest that the summer rainfall should create favourable rather than unfavourable conditions for growth of heath vegetation. In coastal Queensland, where there is a marked coincidence of

summer rainfall with high air temperatures, the authors have observed that growth of heath plants tends to coincide with that at Keith and is exceptionally vigorous at this time.

TABLE 4
VARIATION OF LEAF: STEM RATIO WITH AGE

Species	Leaf: Stem (dry wt.) (%)					
	4 months	9 months	15 months	27 months	45 months	7–8 years
Banksia ornata	∞*	∞*	∞*	1200	790	92
Banksia marginata	170	225	290	?	88	34
Casuarina pusilla	∞*	∞*	192	216	117	59
Phyllota sp.	200	270	123	?	?	84
Hibbertia stricta var.	216	203	104	?	?	59

* No stems apparent.

Not every terminal or lateral shoot produces new growth every year. New shoots appear scattered over the shrubs; these shoots then grow, their maximum growth

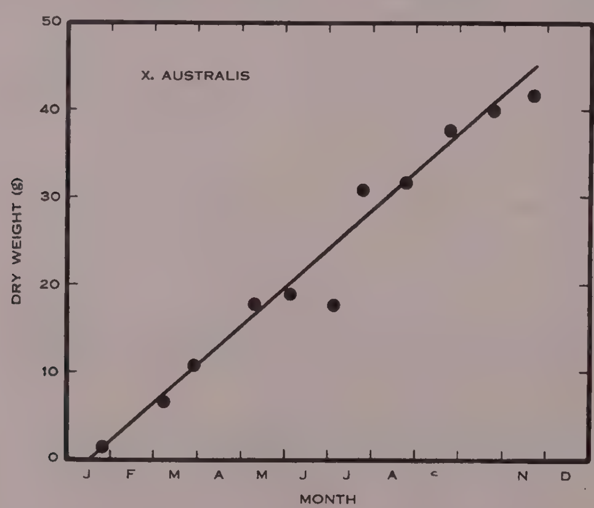

Fig. 10.—Dry weight, at intervals shown, of leaves regenerating from underground root stocks of *Xanthorrhoea australis* which survived a fire in January 1954.

being apparently dependent on the climatic conditions during the months January–March. Nevertheless, the total amount of stems of the plant is continuously increasing. Not only are shoots of the current year being added, but the older branches are slowly but continually increasing in girth. The amount of leaf added every year

increases with the age, and consequently the size, of the bush. These leaves reach their maximum area and dry weight during their first year of growth and little if any change occurs in subsequent years. However, as leaf-fall occurs within 2–4 years after their initiation, the annual increment of leaf must be considered in relation to annual decrement of leaf-fall (see Fig. 9). Thus as the plant ages, the proportion of leaf to stem gradually decreases (Table 4).

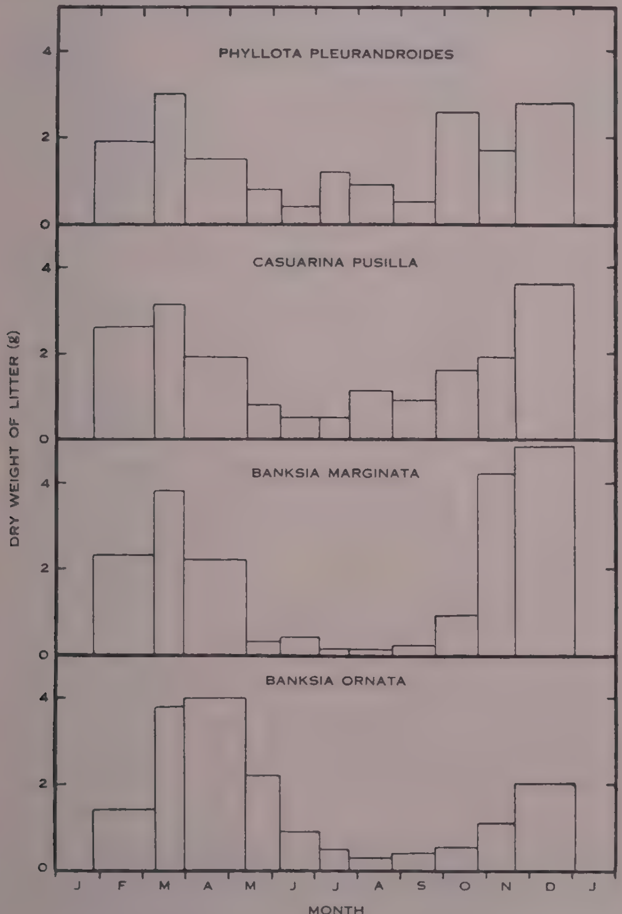

Fig. 11.—Amount of litter-fall of four species of the heath at times indicated. Tins ($5\frac{1}{2}$ by 4 in.) were placed under 10 random bushes of each species during 1954.

Should the vegetation be burnt, many of the larger species regenerate from underground rootstocks. These contain a considerable reserve of food which is mobilized to produce the aerial vegetative shoots. Growth under these conditions is continuous and apparently independent of the climatic conditions. This is illustrated in Figure 10, which shows the dry-weight production of *X. australis* following a fire.

To produce this graph, 50 random specimens of this species were harvested in sets of five during each month of 1954.

(c) *Leaf-fall*

The leaves of most species are usually retained on the shrubs for 2–4 years before they senesce and fall (see Fig. 9). Leaves will fall when 2 years old if drought conditions have prevailed; wet years will favour the retention of leaves for as long as 4 years. Although leaves are shed continually throughout the year, the majority fall towards the end of exceptionally dry periods, during the summer or after a drought during spring (see Fig. 11). Very few fragments of stems are shed, even from more brittle plants like *Phyllota* spp. Sometimes a branch or even a whole plant may die; the leaves fall, while the stems remain erect where they disintegrate very slowly.

TABLE 5

DRY WEIGHTS PER 100 LEAVES GATHERED FROM ANNUAL LAYERS OF LEAF LITTER

Species	Distinguishable Layers	Dry Weight in grams per 100 leaves			
		July 1951	Sept. 1951	Dec. 1951	Mar. 1952
Banksia ornata					13·25*
	1	10·05	9·95	10·89	9·90
	2	7·12	7·53	5·55†	3·44†
Banksia marginata					3·94*
	1	4·01	4·31	2·97	3·34
	2	3·27	—†	—	—
Casuarina pusilla	1	0·92	1·07	0·99	0·72
Phyllota pleurandroides	1	0·11	0·10	0·11	0·12

* Recent litter.
† Greatly decomposed.

(d) *Litter Decomposition*

As it is possible to distinguish the annual layers of litter from the two species of *Banksia*, some idea of the rate of decomposition of this litter may be gained. Table 5 indicates that $1\frac{1}{2}$–$2\frac{1}{2}$ years pass before the leaves are completely decomposed. Decomposition is slow during the first year, but becomes rapid in the second as the layer approaches the surface of the soil. Microbial activity appears to be optimal during spring when surface moistures are near their maximum and temperatures are 10–20°C. Rate of decomposition is markedly influenced by the season, for decomposition was retarded by the long dry summer and poor winter rains of 1950 compared with the more favourable seasons of 1951.

B. ornata, *B. marginata*, *Casuarina pusilla*, *X. australis* and *Phyllota* spp. contribute most to the annual fall of litter. Dead leaves of *Xanthorrhoea* which

remain on the plant above ground are removed from the site of greatest microbial decomposition for a considerable number of years; little return of nutrients can be expected from this source. Most other species of the heath provide some litter but never in appreciable quantities.

(*e*) *Flowering Rhythms*

The flowering period of each species recorded in the heath vegetation is indicated in Appendix I. These observations are summarized in Figure 12, which shows the number of species flowering in each month throughout the year. Most species flower and fruit during spring and early summer, but flowering in some (especially the more

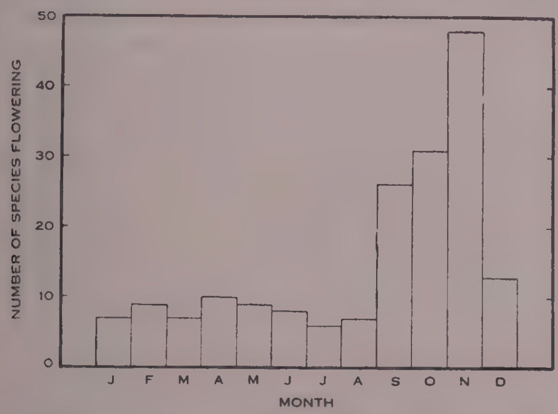

Fig. 12.—Histogram showing the number of species found flowering during each month of the year. The data summarize the observations from 1950 to 1954.

prominent shrubs *B. ornata*, *B. marginata*, *C. pusilla*, and *Phyllota* spp.) does not occur until late summer, autumn, or even midwinter. A few, e.g. *Boronia caerulescens* and *Hibbertia stricta*, flower irregularly throughout the year but produce a flush of flowers during the spring.

The maximum flowering period occurs during spring when (1) the mean air temperatures are 55–60°F and (2) there is a considerable reserve of soil moisture. The number of species flowering is reduced both by low winter temperatures and by high summer temperatures; autumn temperatures appear favourable to flowering, but flowering is reduced by the small supply of soil moisture. Most of the species which flower during summer and autumn are deep-rooted species which rely for moisture on the reserves in the clayey B horizon.

These observations agree essentially with those of Patton (1933) in his studies on the heath vegetation at Cheltenham. However, the flush of flowering at Keith does not begin until September and reaches its peak in November, whereas at Cheltenham the flush begins in August, reaches its peak in October, and is falling sharply by November.

(*f*) *Some Statistics of the Vegetation*

(i) *Size of Quadrats.*—A species-area curve was constructed by recording the number of species which were growing in random quadrats of increasing area in a stand of heath 10 years old.* By the use of the technique described by Cain (1943), the minimum size of the quadrat which gives a satisfactory sample of the vegetation was estimated. This quadrat had a size of 22 sq. ft and contained, on the average, 18 of the 37 species which were recorded in the stand.

Although this area sampled adequately the majority of the species within the stand, it failed to give a reasonable sample of two of the co-dominant species, *B. ornata* and *B. marginata*, which were found in only 5 and 15 per cent. respectively of the quadrats. In quadrats 10 sq. yd in area, the maximum size examined above, specimens of *B. ornata* were recorded in only 20 per cent. of the quadrats, and in quadrats of 25 sq. yd in 60 per cent. of the quadrats. Statistics of the larger species were collected from quadrats of 25 sq. yd, while the smaller species were examined in a random sub-quadrat with a minimum area of 22 sq. ft.

(ii) *Number of Quadrats.*—A series of random quadrats of the minimum area determined above were examined in a 10-year-old stand of heath and a species–number curve constructed. The minimum number of such quadrats necessary for satisfactory analysis of the vegetation was determined by the technique used by Cain (1943) to be at least four. In practice many more quadrats of both minimum area and of larger area (25 sq. yd) have been used in this survey.

VI. Discussion

The two outstanding characteristics of the heath vegetation, viz.: (1) its summer growth in a mediterranean-type climate, and (2) its invariable occurrence on very infertile soils, may be connected with its evolutionary history. Many of the genera of the Australian heath can be traced in fossil records back to the early Tertiary era when they became prominent and widespread across the peneplain of southern Australia before the Miocene period. During the Miocene, the sea invaded the land to the north of the Great Australian Bight and in south-eastern South Australia and western Victoria, thus isolating the flora into three areas where speciation continued along separate paths. It is not known what soil conditions existed prior to the Miocene, but after this period climatic conditions prevailed which produced lateritic podsols over the non-calcareous areas, i.e. in general the areas which had not been invaded by the Miocene seas. The lateritic podsols are all heavily leached and are consequently acid in pH and very low in fertility. Today fossil remnants of these soils support excellent examples of the Australian heath element (e.g. much of the south-west of Western Australia; the peneplain of Kangaroo Island, and the ridge tops in the Mt. Lofty Ranges of South Australia; the ridge tops of the Hawkesbury Sandstone Formation near Sydney, N.S.W.)—probably almost identical with that supported when the soils were formed. If one assumes that the same climatic conditions then existed as those which prevail in areas where lateritic podsols are being formed at the present time, the climate must have been consistently much wetter throughout the year than it is

* Age of a stand is dated from the time of the last fire.

at present and possibly much warmer. The most favourable conditions for growth of the heath would probably have been during summer, a situation seen today in the heath of south coastal Queensland. Thus it appears that the heath element was well developed during the Pliocene period on lateritic podsols under a climate with appreciable rainfall throughout the year and with probably much warmer temperatures, all of which favoured summer growth. Since that time southern Australia has undergone a period of extensive block faulting which has led to the dissection of the extensive lateritic peneplains; now only relict areas of the Pliocene lateritic podsol remain. The heath element has persisted on these relict soils and has invaded more recent soils wherever the soil nutrient and pH conditions have approximated that of the original lateritic podsols. Such sites are found wherever the parent rock is initially poor in plant nutrients—e.g. (1) sandstones and quartzites, (2) on sandplains and dunes derived either from a redistribution of the A horizon of the Pliocene lateritic podsols or from a redistribution of old coastal dune systems, or (3) wherever the climatic conditions have induced a considerable degree of leaching of parent nutrients from the developing soil. All other sites, though undoubtedly still low in phosphorus and nitrogen, show a much higher level of plant nutrients than the lateritic podsols and their allies, and they support a herbaceous instead of a sclerophyllous understorey.

Not only have soil conditions undergone considerable change, but the climate has changed until there now occurs a typical mediterranean climate with, hot dry summers alternating with cool, wet winters. Under such a climatic regime, only those species of the Pliocene flora which possessed mechanisms to conserve enough moisture during the winter and spring periods to enable a reserve to be present during much of the summer growing period could survive. The soil moisture storage under the heath vegetation during the summer period has been discussed by Specht (1953). A few geophytes, hemicryptophytes, etc. are adapted to spring growth. No doubt a great number of species disappeared, especially during the rigours of the Arid period when the mediterranean climate became much more severe than it is today (Crocker and Wood 1947). We now see a flora which has been adapted to flourish on soils very low in fertility and whose growth rhythm is markedly out of phase with the present annual climatic cycle.

VII. Acknowledgments

The authors wish to express their gratitude to Professor J. G. Wood, who initiated this project and offered his advice throughout. The Australian Mutual Provident Society, who kindly loaned about 320 acres of land to the University of Adelaide for the project, are deserving of sincere thanks.

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Appendix I

This appendix tabulates the species of angiosperms recorded in the heath vegetation on the Makin sand near Keith, South Australia. The nomenclature and arrangement of the families are according to J. M. Black's (1943–57) "Flóra of South Australia" unless stated otherwise. A set of herbarium specimens of the species recorded has been deposited in the Herbarium of the Department of Botany, University of Adelaide. Raunkiaer's (1934) life form and leaf size categories are indicated for each species.

Raunkiaer's Life Form Key

Megaphanerophytes	(M.M.)	Geophytes	(G)
Mesophanerophytes	(M)	Halophytes	(HH)
Nanophanerophytes	(N)	Therophytes	(Th)
Chamaephytes	(Ch)	Epiphytes	(E)
Hemicryptophytes	(H)	Succulents	(S)

Raunkiaer's Leaf Size Key

Leptophyll	(L)	Mesophyll	(Mes)
Nanophyll	(N)	Macrophyll	(Mac)
Microphyll	(Mic)	Megaphyll	(Meg)

Key to the General Distribution of the Species

Continuous throughout the area	(Cont)
Confined to the sand plains	(SP)
Confined to the low sand ridges	(SR)
Confined to the lee face of steep sand dunes	(LSD)
Confined to the crest of steep sand dunes	(CSD)
Found only in old stands of heath	(OS)
Rare in any situation	(Rare)

Flowering Periods of Each Species

——— Buds obvious   □□□ Flowering

Species	Life Form	Leaf Size	Distribution	Month of Flowering: Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Family Gramineae															
Stipa McAlpinei Reader	Th	L–N	Cont										<	□□□	>*
S. semibarbata R. Br.	H	L–N	Cont										<	□□□	>
Danthonia geniculata J. M. Black	H	L–N	OS										<	□□□	>
D. setacea R. Br.	H	L–N	Cont										<	□□□	>
Neurachne alopecuroides R. Br.	H	L–N	Cont										<	□□□	>
Triodia irritans R. Br.	Ch	N	Cont										——<	□□□	>†
Eragrostis brownii (Kunth) Nees	H	L–N	LSD									<	□□□	□>	
Amphipogon caricinus F. Muell.[1]	G	L–N	Cont										<	□□□	>

APPENDIX I (*Continued*)

Species	Life Form	Leaf Size	Distribution	Month of Flowering											
				Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Family Cyperaceae															
Lepidosperma laterale R. Br.	H	N	Cont	<	□□□	□□□	□□□	>†							
L. carphoides F. Muell. ex Benth.	H	L–N	Cont	<	□□□	□□□	□□□	>†							
Schoenus tepperi F. Muell.	H	L	Cont	<	□□□	□□□	□□□	>							
Family Restionaceae															
Hypolaena fastigiata R. Br.	G	L–N	Cont										—	—<□	□□>
Lepidobolus drapezocoleus F. Muell.	G	L–N	Cont										—	—<□	□□>
Family Centrolepidaceae															
Centrolepis strigosa (R. Br.) R. & S.	Th	L	OS									<□□	□□□	□□>	
Family Liliaceae															
Lomandra glauca (R. Br.) Ewart	H	N	CSD								—	—<	□□□	>	
L. leucocephala (R. Br.) Ewart	H	Mic	CSD								—	—<	□□□	>	
L. juncea (F. Muell.) Ewart	G	Mic	Cont			—<	□□□	□□□	>						
Thysanotus patersonii R. Br.	G	L–N	Cont									—	<□□	□□>	
T. dichotomus (Labill.) R. Br.	G	L–N	Cont	□□>										—<□□	□□□
Laxmannia sessiliflora Dcne	H	L	Cont											<□□□	>
Xanthorrhoea australis R. Br.	N	Mic–Mes	Cont								—	—	<□□	□□□	>*
Tricoryne elatior R. Br.	G	L–N	Cont	□□>										—<	□□□
Dianella revoluta R. Br.	G	N	CSD												‡

* Observed flowering only after a fire. † Not flowering every year. ‡ Not observed flowering.

[1] See Williams (1953, p. 52).

APPENDIX I (*Continued*)

Species	Life Form	Leaf Size	Distribution	Month of Flowering: Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Family Orchidaceae															
Thelymitra antennifera Hook. f.	G	L	Rare								——<	□□□	>		
Prasophyllum patens R. Br.	G	N	Cont								——<	□□□	>		
Lyperanthus nigricans R. Br.	G	N	Cont								——<	□□□	>*		
Caladenia deformis R. Br.	G	L	Rare								——<	□□□	>		
Diuris maculata Sm.	G	L	Rare								——<	□□□	>		
Family Casuarinaceae															
Casuarina pusilla Macklin	N	L	Cont	——	<□□	□□□	□□□	□□□	>§						——
C. muelleriana Miq.	N	L	LSD	——	<□□	□□□	□□□	□□□	>§						——
Family Proteaceae															
Adenanthos terminalis R. Br.	N	L	Cont	□□>							——	——<	□□□	□□□	□□□
Conospermum patens Schlecht.	N	L	Cont	□□>									——<	□□□	□□□
Persoonia juniperina Labill.	N	L	Cont											——<	□□>
Hakea rostrata F. Muell.	N	N	Rare									——<	□□□	□□□	>
H. ulicina R. Br. var. *latifolia* J. M. Black	N	N	Cont									——<	□□□	□□□	>
H. muelleriana J. M. Black	N	N	Cont								——	——<	□□□	□□□	>
Banksia marginata Cav.	N	N	Cont		——	——<	□□□	□□□	>§						
B. ornata F. Muell.	N	Mic	Cont		——	——	——	——	<□□	□□□	□□□	>§			
Isopogon ceratophyllus R. Br.	N	N	Cont									<	□□□	>	
Family Santalaceae															
Exocarpos sparteus R. Br.[2]	N–M	L	LSD							—	——<	□□□	>		
Eucarya acuminata (R. Br.) Spr. & Summ.	N	N	Rare										——<	□□□	>

APPENDIX I (*Continued*)

Species	Life Form	Leaf Size	Distribution	Month of Flowering: Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Family Phytolaccaceae															
Gyrostemon australasicus (Moq.) Heimerl.	N	L–N	SR									—	——<	□□□	□>
Family Aizoaceae															
Carpobrotus sp.‖	S	Mic	Rare								<	□□□	□>		
Family Lauraceae															
Cassytha glabella R. Br.	E	—	Cont	——	——	——<	□□□	>							
C. pubescens R. Br.	E	—	Cont	——	——	——<	□□□	>							
Family Cruciferae															
Stenopetalum lineare R. Br.	H	L	LSD									<	□□□	>	
Family Droseraceae															
Drosera whittakeri Planch.	G	N	Cont								——<	□□□	>		
D. planchonii Hook. f.	G	L	SR								——<	□□□	>		
Family Pittosporaceae															
Bursaria spinosa Cav.	N–M	L–N	CSD	□□□	>									——	——<
Billardiera cymosa F. Muell.	N	N	LSD									<	□□□	>	

* Observed flowering only after a fire. § Fruits mature in October to November. ‖ Under revision by S. T. Blake.

² See La Billardière (1799, Vol. 1: 155, t. 14).

APPENDIX I (*Continued*)

Species	Life Form	Leaf Size	Distribution	Month of Flowering											
				Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Family Leguminosae															
Gompholobium minus Sm.	Ch	L	Cont								——	<□□	□□□	□□□	>
Daviesia brevifolia Lindl.	N	L	Cont								——<	□□□	>		
Phyllota pleurandroides F. Muell.	N	L	SR	——<	□□□	>									
P. remota J. H. Willis[3]	N	L	SP	——<	□□□	>									
Dillwynia hispida Lindl.	N	L	Cont									——<	□□□	□□□	>
Family Rutaceae															
Zieria veronica F. Muell.	N	L	LSD								——<	□□□	□□□	□□□	>
Boronia caerulescens F. Muell.	N	L	Cont								——<	□□□	□□□	□□□	>
Correa rubra Sm.	N	N	Cont	<	□□□	□□□	□□□	□□□	□□□	>					
Family Polygalaceae															
Comesperma calymega Labill.	H	L	Cont											——<	□□>
Family Euphorbiaceae															
Poranthera microphylla Brogn.	Th	L	Cont									<	□□□	□>*	

APPENDIX I (*Continued*)

Species	Life Form	Leaf Size	Distribution	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Family Rhamnaceae															
Spyridium subochreatum (F. Muell.) Reiss. var. *laxiusculum* J. M. Black	N	L	Cont												
Cryptandra tomentosa Lindl.	N	L	Cont												
C. leucophracta Schlecht.	N	L	SR												
Family Dilleniaceae															
Hibbertia sericea (R. Br.) Benth. var. *scabrifolia* J. M. Black	N	L	Cont												
H. stricta R. Br. var. *glabriuscula* Benth.	N	L	Cont												
H. virgata R. Br.	N	L	Rare												
Family Violaceae															
Hybanthus floribundus (Lindl.) F. Muell.	N	L-N	LSD												
Family Thymelaeaceae															
Pimelea octophylla R. Br.	N	L	Cont												
P. phylicoides Meisn.	N	L	Cont												

* Observed flowering only after a fire.

[3] See Willis (1957, p. 191).

APPENDIX I (*Continued*)

Species	Life Form	Leaf Size	Distribution	Month of Flowering											
				Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Family Myrtaceae															
Baeckea ericaea F. Muell.	Ch	L	Cont					—	—<	□ □	□ □	□□□	□□□	>	
B. behrii (Schlecht.) F. Muell.	N	L	LSD											—<	□□>
Leptospermum coriaceum (F. Muell.) Cheel.	N	L–N	SR								—<	□□□	□□□	□□□	>
L. myrsinoides Schlecht.	N	L	Cont									—	—<	□□□	>
Kunzea pomifera F. Muell.	Ch	L–N	Rare									—	—<	□□□	>
Eucalyptus baxteri (Benth.) Maid. & Blak.	M	Mic–Mes	LSD								—	—	—<	□□□	>
Calytrix tetragona Labill.[4]	N	L	Cont									—	—<	□□□	>
C. alpestris (Lindl.) Court[5]	N	L	Cont							—	—<	□□□	□□□	□□□	>
Family Haloragaceae															
Loudonia behrii Schlecht.	H	L	CSD										—<	□□□	>
Haloragis tetragyna (Labill.) Hook.	H	L	Cont										<	□□□	>
Family Epacridaceae															
Styphelia exarrhena F. Muell.	N	L	Cont			—	—<	□□□	□□□	>					
Astroloma humifusum (Cav.) R. Br.	Ch	L	Cont									—	—<	□□□	>
A. conostephioides (Sond.) F. Muell.	N	L	Cont				—	—	—<	□□□	□□□	□□□	□□□	□>	
Leucopogon costatus F. Muell.	N	L	Cont						—	—<	□□□	□□□	□□□	>	
L. woodsii F. Muell.	N	L	Cont		—	—	—<	□□□	□□□	>					
L. clelandii Cheel.	N	L	Cont					—<	□□□	□□□	>				
Acrotriche affinis DC.	Ch	L	Cont						—	—<	□□□	>			
Brachyloma ericoides (Schlechtd.) Sond.	N	L	Cont					—<	□□□	>					

APPENDIX I (*Continued*)

Species	Life Form	Leaf Size	Distribution	Month of Flowering											
				Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Family Scrophulariaceae															
Euphrasia collina R. Br.	H	L	Cont								——<	□□□	□□□	>	
Family Rubiaceae															
Opercularia scabrida Schlechtd.	H	L	Cont											——<	□□>
Family Campanulaceae															
Wahlenbergia gracilenta Lothian	Th	L	Rare									——<	□□□	□>	
Lobelia gibbosa Labill.	Th	L	LSD	□>											<□
Family Goodeniaceae															
Goodenia geniculata R. Br.	Ch	N	Cont										——<	□□□	>
G. robusta (Benth.) Krause	H	Mic	LSD										——<	□□□	>
Dampiera marifolia Benth.	H	N	Cont										——<	□□□	>

[4] See La Billardière (1806, Vol. 2: 8, t. 146).

[5] See Court (1957, p. 176).

APPENDIX I (*Continued*)

Species	Life Form	Leaf Size	Distribution	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
				Month of Flowering											
Family Stylidiaceae															
Stylidium majus (Sm.) Druce	H	N	Cont										——<	□□□	>
Family Compositae															
Olearia lepidophylla (Pers.) Benth.	N	L	Rare				<	□□□	□>						
O. ciliata (Benth.) F. Muell.	Ch	L	Cont									——<	□□□	>	
Helichrysum obtusifolium F. Muell. & Sond.	Ch	L	Cont								——<	□□□	□□□	>	
H. scorpioides (Poir.) Labill.	Th	N–Mic	LSD										——<	□□□	>
H. baxteri A. Cunn.	Ch	L	SR										—	—< □	□□>
H. leucopsidium DC.	Ch	N	LSD									—	——<	□□□	□>
H. blandowskianum Steetz	Ch	N	Cont	□>										——<	□□□
Toxanthus muelleri (Sond.) Benth.	Th	L	OS								<	□□□	□>		
Vittadinia triloba (Gaudich.) DC.	Th	L	Rare											<□□	□□>

Appendix II

The cryptogamic flora, which has been recorded in the heath vegetation on the Makin sand near Keith, South Australia, is listed below.

Algae

Cylindrocapsa geminella Wolle.—Prominent in hollows between vegetation during winter.

Musci

Bryum argenteum (Heslw.) Dix.—Rare.
Tortella calycina (Schwaeg.) Dix.—Common.

Lichens

Cladonia aggregata (Sw.) Ach.—Common.
C. fimbriata (L.) E. Fr.—Common.

Fungi

Ascomycetes

Geoglossum nigritum Fr.
Poronia punctata L.—On kangaroo dung.
Sarcosphaera sp.—Common especially after a fire.

Basidiomycetes

Boletus sp.
Coltricia cinnamomea (Jacq.) Murr.
C. oblectans (Berk.) Cunn.
Coriolus sanguineus (Fr.) Cunn. syn. *Trametes cinnabarina* Berk.
Cortinarius fibrillosus Clel.
C. subcinnamoneus Clel.
Flammulla paludosa Clel.
Geastrum campestre (Morgan) Kembley & Lee.
Lycoperdon gunnii Berk.
L. spadiceum Pers.
L. pusillum Pers.
Naucoria arenacolens Clel.
N. verona-brunneus Clel.
Psathyra sonderiana Berk.
Psilocybe subammophila Clel.
Tremella mesenterica (Retz) Fr.
Tulostoma albicans White.

Heterobasidiae

Aecidium goodeniacearum stage of *Puccinia saccardoi* on *Goodenia geniculata*

DARK ISLAND HEATH (NINETY-MILE PLAIN, SOUTH AUSTRALIA)

II. THE EFFECTS OF MICROTOPOGRAPHY ON CLIMATE, SOILS, AND VEGETATION

By Patricia Rayson*

[*Manuscript received February* 28, 1957]

Summary

The topography of the experimental area at Dark Island is described as a series of crescentic sand dunes formed under the influence of westerly winds and separated by undulating sandplain.

Variation in the heath vegetation of the area in relation to topography was described by means of the varying densities of 12 representative species. These densities indicated the individual growth tolerances of the vegetation components.

One hundred and twenty-six quadrats sampled from different topographical positions were sorted into homogeneous groups by the method of positive interspecific correlation. The four resultant vegetation communities were located respectively on eastern dune slopes, western dune slopes, sandplain, and in scattered sites.

Examination of soil texture, rainfall incidence, and average daily hours of direct sunlight in relation to topography showed that three microhabitats can be separated: namely, eastern and western dune slopes and the sandplain. Eastern dune slopes have the most favourable growth conditions, western the least favourable.

Neither the vegetation communities nor the microhabitats could be sharply delimited. The gradual changes of soil and microclimate produced a varying but continuous vegetation pattern. This pattern depended on the growth tolerances of different species and probably also on interspecific competition for the more favourable growth sites.

I. Introduction

In the first paper of this series (Specht and Rayson 1957) a general description of the heath vegetation and its environment has been given.

Of the 104 species of angiosperms collected in the area 65 were continuous throughout the area, but approximately 20 per cent. were restricted to the sand dunes (viz. 6 species on the sand ridge, 5 on the crest, and 13 on the lee face). Eleven species were rare in any position. The occurrence of a large proportion of these restricted species in the same positions was repeated on every dune. In addition, species with an apparently continuous distribution throughout the heath varied in density or rate of growth, depending on their position in relation to the dune systems.

In the present paper, the distribution of the major indicator species with topography, the communities into which these species fall, and the microhabitat imposed by the topography, on which the plant distribution depends, are discussed.

II. The Distribution of Representative Heath Species

(a) *Method*

(i) *Selection of the Site*.—After a preliminary subjective survey of all dunes within an area of 5 sq. miles, one barchanoid dune, with its major axis running due

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north and south and with a height of approximately 50 ft of sand above clay, was selected for detailed mapping. The dune had been uniformly burned 9 years previously. The vegetation pattern was similar to that of all the other dunes of similar height in the area.

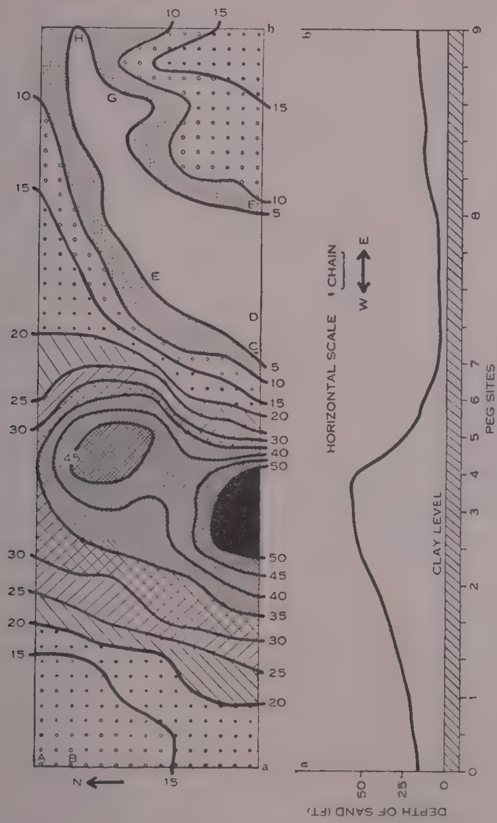

Fig. 1.—Relief map of a portion of a barchanoid dune. Altitudes in feet of sand above the clay level were measured with an aneroid surveyor's altimeter, and checked by auger borings at sites *A–H*. (*A*, clay at 9 ft 8 in.; *B*, 10 ft 4 in.; *C*, 5 ft 1 in.; *D*, 4 ft; *E*, 5 ft 8 in.; *F*, 4 ft 7 in.; *G*, 4 ft 10 in.; *H*, 5 ft.) In cross section, *a–b*, the vertical scale is 3 times the horizontal scale. Soil samples for mechanical analysis were taken from peg sites 1–9.

The angle of the west-facing windward slope was 5° and that of the eastern leeward slip face was 22°. The dune was roughly Y-shaped, with a slight central rib in the western slope and the crest forming a broad shallow crescent, 15 ch wide at its extremities. Another low dune, approximately 25 ft high, was situated a few chains to the east.

A baseline, 20 ch long, running due east and west, and extending on to the sand-plain on both sides, was established across the centre of the dune and pegged at 1-ch intervals. On the northern side of this baseline, a rectangle 6 by 20 ch in extent, was pegged in areas of 1 ch square.

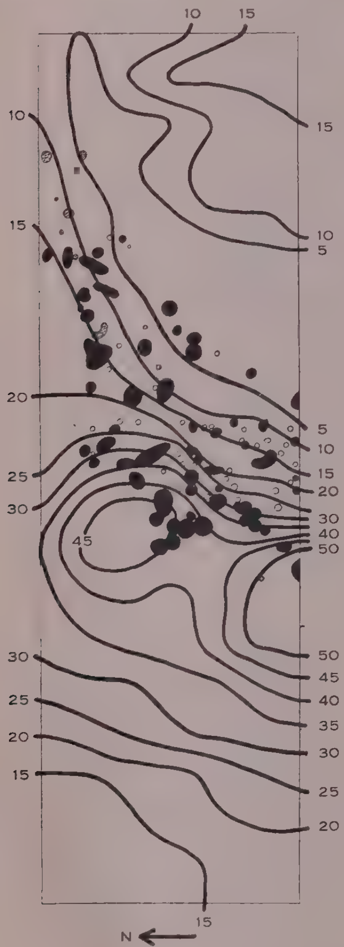

Fig. 2

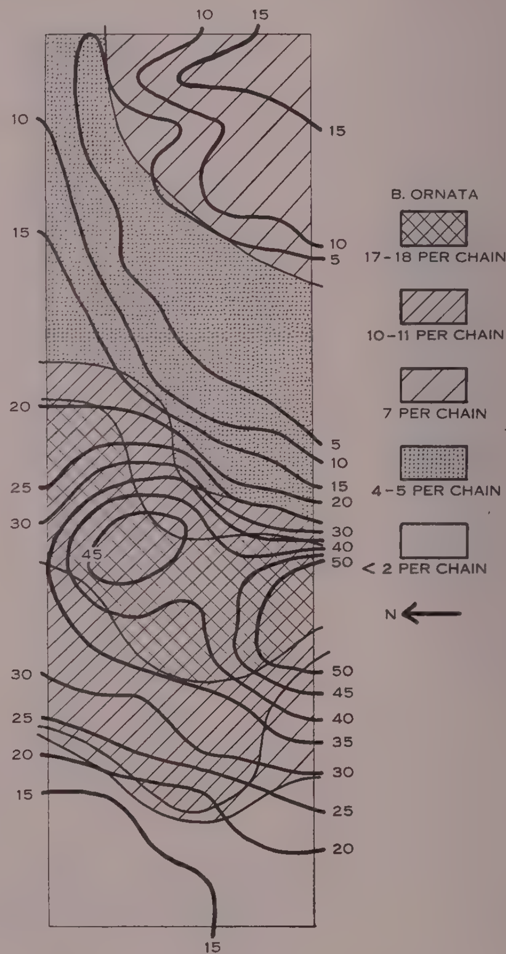

Fig. 3

Fig. 2.—A map of portion of a sand dune showing the distribution of clumps of *Eucalyptus baxteri* in relation to the topography. Stippled areas denote thickets of bush plants less than 3 ft high. Fig. 3.—The distribution of *Banksia ornata* in relation to topography.

(ii) *Construction of the Relief Map.*—The depth of sand over clay was established at a basal point by an auger boring. Readings were taken with an aneroid surveying altimeter at all peg sites and recorded as depth of sand over clay by difference from basal point. The altimeter readings were then checked by further auger borings in various positions on both sides of the dune. The chain grid was corrected for slope and the relief map (Fig. 1) was constructed.

(iii) *Vegetation Maps.*—The position and size of clumps of *Eucalyptus baxteri*, the only tree species, were mapped in detail. The density of 12 representative species was determined from 126 quadrats, each 1 ft by 1 ch, run from peg to peg in a north-south direction. Maps were constructed connecting points of the same density of aerial shoots of each species. This is a modified version of the isonomes used by

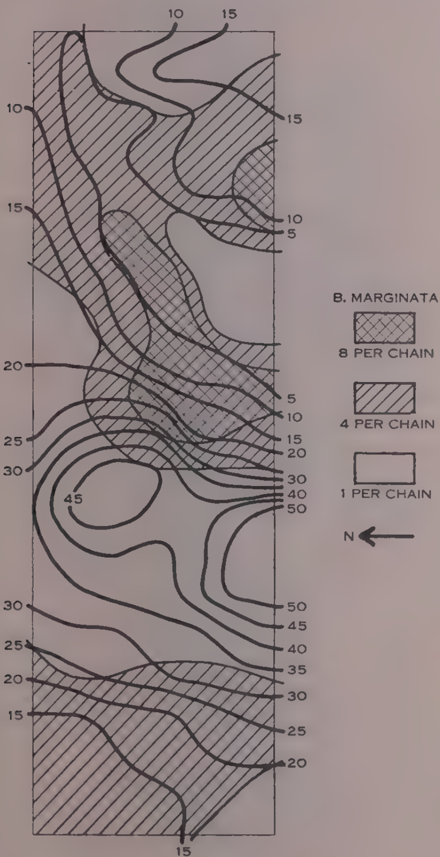

Fig. 4

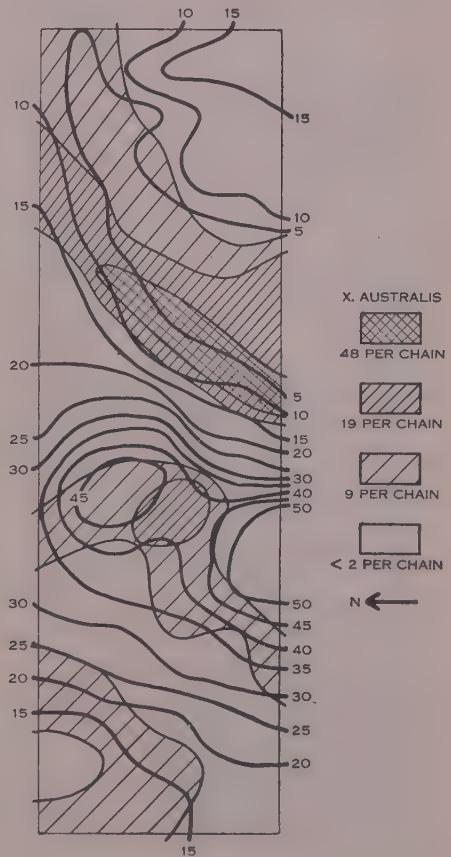

Fig. 5

Fig. 4.—The distribution of *Banksia marginata* in relation to topography.
Fig. 5.—Variations in the density of *Xanthorrhoea australis* with topography.

Pidgeon and Ashby (1942). However, in this case the densities were not expressed as a percentage of the total vegetation. Some danger of bias was introduced with the use of non-random quadrats (Goodall 1952), but the estimates of density calculated for the major species from random quadrats on the sandplain (Specht 1953) agreed closely with estimates prepared from these non-random sandplain quadrats. The problem of aggregation of vegetatively reproducing species could not be overcome without substituting dry weight for density. The work which this would have involved was impossible to encompass.

(b) Results

Distribution of individual species derived from the isonome maps are detailed under (i)–(xi) below.

(i) Eucalyptus baxteri.—This occupied the crest and the eastern face of the dune, fringing the lee plain in a crescent shape. The plants thinned to very stunted thickets at the points of the crescent (Fig. 2).

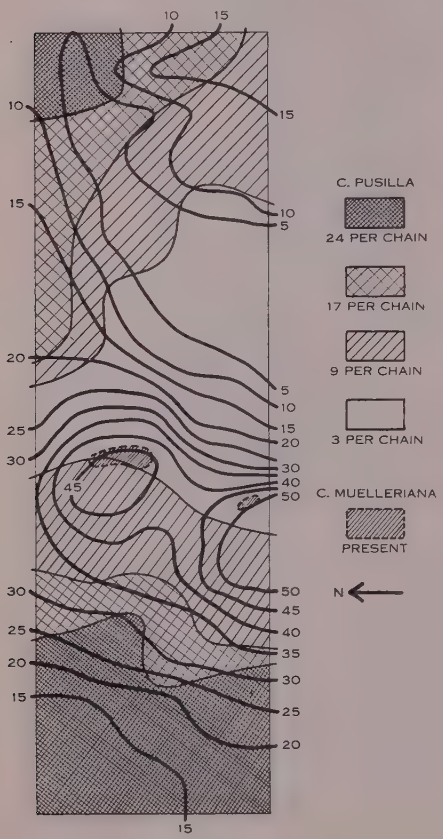

Fig. 6

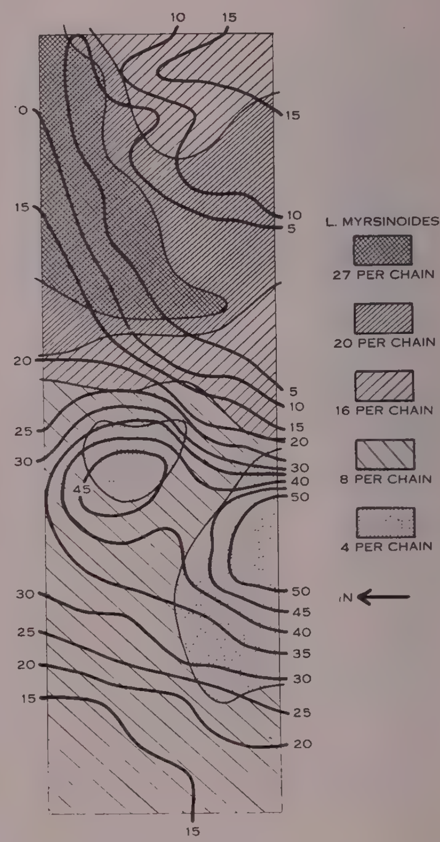

Fig. 7

Fig. 6.—Variations in the density of *Casuarina pusilla* with topography. Presence of *Casuarina muelleriana* is marked.

Fig. 7.—Variations with topography in the density of *Leptospermum myrsinoides*.

(ii) Banksia ornata.—This species was continuous throughout the area, but showed an appreciable increase in numbers on deep sand ridges; density was slightly higher on the shallow, sheltered lee plain than on normal sandplain (Fig. 3). The height of the bushes of the same age varied considerably with their position; average height was 3 ft on the sandplain and lower western slopes, 1 ft 6 in. on the most exposed parts of the windward slopes, and 4 ft 6 in. on the leeward slopes.

(iii) Banksia marginata.—This species chiefly occupied the sandplain and the lower dune faces; numbers decreased appreciably on the western slopes of the ridges. This record of the density of aerial shoots was complicated by aggregation due to vegetative reproduction; the increase in numbers at the fringe of the lee plain (Fig. 4) was probably an expression of increased growth common to all plants in this position.

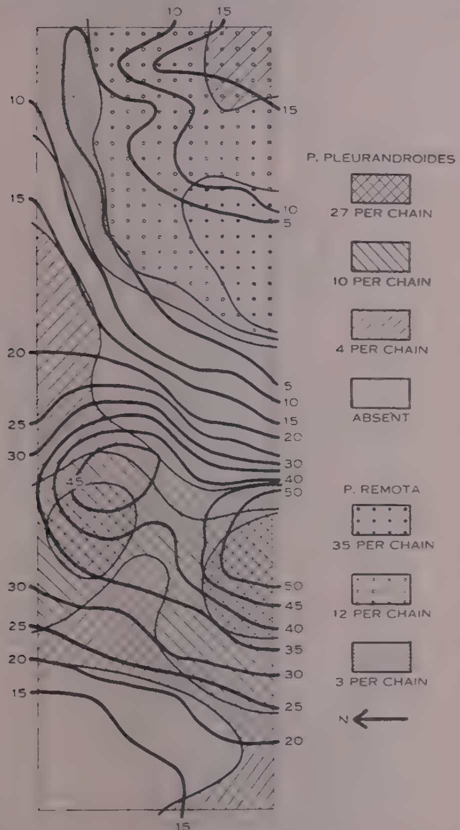

Fig. 8

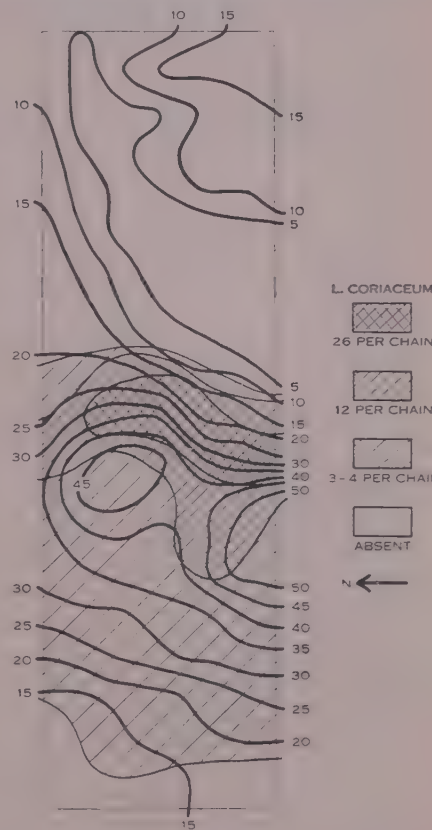

Fig. 9

Fig. 8.—The distribution with topography of the two species of *Phyllota*.
Fig. 9.—The distribution of *Leptospermum coriaceum* in relation to topography.

(iv) Xanthorrhoea australis.—Marked aggregation of stocks complicated examination of this species by the method followed. It was almost absent from the lee face but continuous over the rest of the area (Fig. 5). While the distribution of the clumps of plants was similar, the average number of plants per clump was 1–2 on exposed slopes, 4 on the sandplain, and 10 at the base of the eastern slope.

(v) Casuarina pusilla.—Almost continuous in distribution, this showed its greatest density on normal sandplain. It thinned on exposed sand ridges and the shallower parts of the lee sandplain and was almost absent from the lee slope of larger dunes (Fig. 6).

(vi) Leptospermum myrsinoides.—This was the only species present in all quadrats. The density was greatest on the sandplain and least on the western-facing dune slopes (Fig. 7).

(vii) Phylotta *spp.*—Two distinct species, *P. pleurandroides* and *P. remota*, were found. *P. remota* has a semi-prostrate habit and a deep tap-root, is not resistant to fire, and is propagated solely by seeds. *P. pleurandroides* has smaller, upright

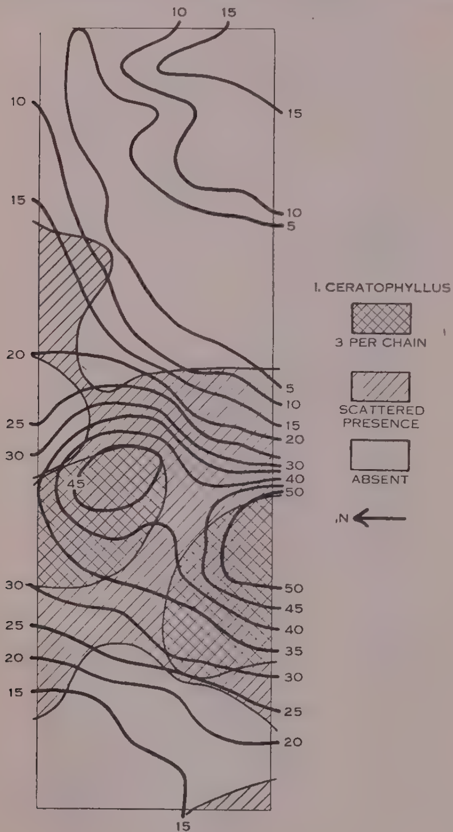

Fig. 10

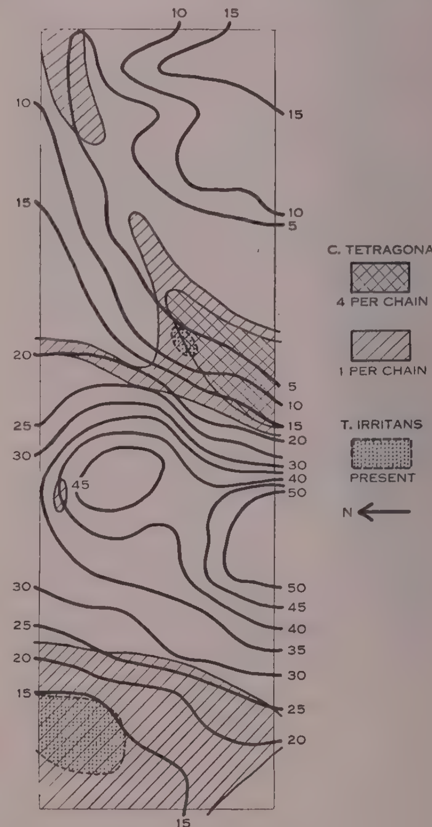

Fig. 11

Fig. 10.—The distribution of *Isopogon ceratophyllus* with topography.
Fig. 11.—The occurrence of *Calytrix tetragona* and *Triodia irritans*.

aerial shoots, is fire resistant, and reproduces vegetatively by buds situated on lateral roots. Original seedling parent plants with deep tap-roots have been found, but in general the shoots were attached by almost horizontal lateral roots, from which vertical roots descended at irregular intervals.

The two species showed a markedly different distribution with topography (Fig. 8), though both were absent from the steep east-facing slope. *P. remota* was distributed throughout the sandplain where the sand depth was less than 15 ft, with the highest density on the shallowest portion of the lee plain. It was present less than

a chain to the west of the area mapped and gave place to *P. pleurandroides* on the crest of the small ridge to the south-east.

P. pleurandroides, which was absent from sand less than 15 ft in depth, occurred extensively on higher ridges, with maximum density on the more exposed faces. An ecotonal mixture of the two species occurred on deeper undulating sandplain and on low ridges. A similar distribution of the two species has been observed throughout the upper south east of South Australia from Meningie to Bordertown.

TABLE 1

THE PERCENTAGE FREQUENCY OF SPECIES IN FOUR HOMOGENEOUS GROUPS OF QUADRATS

Species*	Frequency (%)			
	Group A+B+D (60 quadrats)	Group C+G (46 quadrats)	Group F (7 quadrats)	Group E (13 quadrats)
Eucalyptus baxteri	15	15	100	0
Banksia ornata	90	85	100	100
Banksia marginata	82	98	100	0
Xanthorrhoea australis	68	83	29	93
Casuarina pusilla	100	96	0	100
Leptospermum myrsinoides	100	100	100	100
Phyllota remota	10	65	0	62
Phyllota pleurandroides	80	0	0	54
Leptospermum coriaceum	75	0	100	0
Isopogon ceratophyllus	52	4	43	15
Calytrix tetragona	20	24	43	0
Triodia irritans	3	7	0	0
Casuarina muelleriana	8	0	0	0
Location of quadrats:	North and west dune slopes	Sandplain	Eastern lee face	Scattered

* Nomenclature follows that used in part I of this series (Specht and Rayson 1957, Appendix I.)

(viii) Leptospermum coriaceum.—This species was restricted to the deeper sands of larger dunes. The density and height of bushes increased greatly on the steep eastern slip face (Fig. 9). The average height of bushes on the western slope was 1 ft, on the eastern it was 4 ft 6 in.

(ix) Isopogon ceratophyllus.—This species was also almost restricted to sand dunes. A few plants were found on low ridges in areas of mixed *Phyllota spp.*, but its maximum density occurred on the western face of larger dunes (Fig. 10).

(x) Calytrix tetragona *and* Triodia irritans.—These two species were principally found fringing the base of the eastern dune face (Fig. 11). *Triodia* tended to occur on steeper portions of the slip face, though this was not shown in the area mapped. Both species were found in slightly sheltered depressions throughout the sandplain.

(xi) Casuarina muelleriana.—This species was restricted to the steeper portions of the eastern face of larger dunes (Fig. 6).

III. The Distribution of Communities within the Heath Vegetation

The 126 quadrats recorded were sorted into seven homogeneous groups according to the first method of positive interspecific correlation described by Goodall (1953).

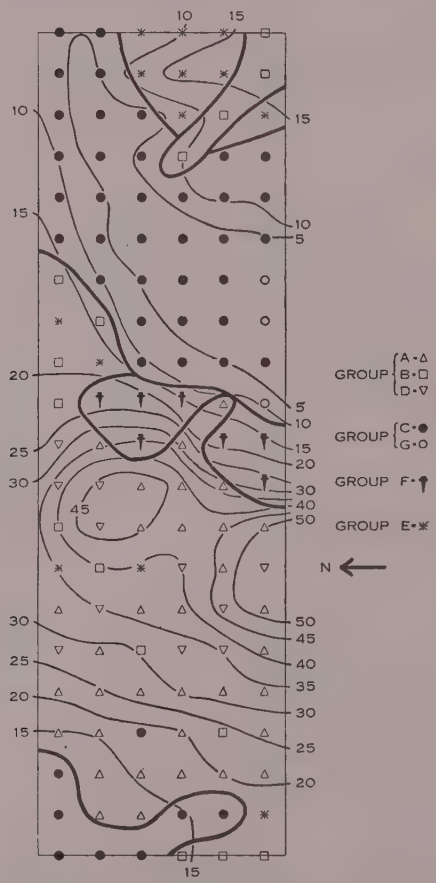

Fig. 12.—The position in relation to the dune topography of the four heath communities derived from sorting 126 quadrats into homogeneous groups by positive interspecific correlation (Goodall 1953).

It was then found possible to recombine three of the groups. These results are shown in Table 1. The position of the quadrats in each homogeneous group was located on the map (Fig. 12), and the boundaries of the resultant communities were drawn. The first three of these four communities can be readily delimited by subjective field observation.

(a) *Groups*

(i) *Group A, B, and D.*—The salient features of this western and northern slope community were the relatively high percentages of *P. pleurandroides*, *L. coriaceum*, and *I. ceratophyllus*, but all the species observed were present to a greater or less extent. Plants tended to be very stunted.

(ii) *Group C and G.*—The distinguishing features of this sandplain community were the high percentage of *P. remota* and the absence of *P. pleurandroides* and of *L. coriaceum*. *I. ceratophyllus* was rare.

(iii) *Group F.*—This was distinguished from the preceding groups by the high percentages of *E. baxteri* and *L. coriaceum*, the absence of *C. pusilla* and *Phyllota spp.*, and the low occurrence of *X. australis*. Within this community, either on this dune or others, the 14 species restricted to the lee face of the dunes have been found.

(iv) *Group E.*—Eight of the total 13 quadrats occupy the low south-eastern ridge; the other five are scattered. It includes most of the mixed *Phyllota* ecotone, but the other distinguishing feature, complete absence of *B. marginata*, is inexplicable.

IV. The Microhabitat

(a) *The Soil*

The varying depth of sandy A horizon has already been discussed and is shown in Figure 1. The texture of sand in relation to topography has been examined by the following method.

Soil samples from depths of 0–$\frac{1}{4}$ in., $\frac{1}{4}$–$\frac{1}{2}$ in., $\frac{1}{2}$–1 in., 1–2 in., 2–3 in., 3–6 in., and 6–12 in., were taken from each of the nine peg points shown in Figure 1. Alternate samples were mechanically sieved, using mesh sizes of 800, 380, 200, 160, 130, and 80 μ. The samples of separate particle size were weighed, expressed as percentages, and cumulative frequency distribution curves of particle size were prepared.

The percentage frequency of particle size for the $\frac{1}{2}$–1 in. samples are recorded in Table 2. In all cases approximately 90 per cent. of the sample was in the fine sand fraction less than 200 μ in diameter. The percentage of fine sand with a diameter of less than 150 μ changed progressively from 30–38 per cent. on western dune slopes to 68–83 per cent. on hill crest and slip face, with sandplain percentages intermediate. A similar degree of difference existed in surface and deeper samples. The frequency distribution curves of particle size for dip slope (site 2) and slip slope (site 4) are shown in Figure 13. They are similar to those prepared by Crocker (1946) for the same general area, although in the present case the percentage of fine sand was higher in all samples.

Soil texture differences, though slight, may have some influence on microhabitat. A higher water-retaining capacity of the finer dune peak and slip face sands may compensate for the run-off which occurs in this position. Internal drainage may be expected to be more rapid in the coarser sands of the western slopes and sandplain. No run-off occurs on the sandplain, and Specht (1953) has shown that little if any soil moisture is lost by internal drainage, as this is halted by the almost impervious clay B horizon; the moisture collecting at the sand-clay interface is available to the deeper-rooting species. On the dunes the predominantly lateral root development indicates that surface soil moisture conditions are most important.

TABLE 2

PERCENTAGE FREQUENCY OF SAND PARTICLE SIZES IN SAMPLES FROM ½–1 IN. DEPTH IN DIFFERENT PROFILES IN SAND DUNE AND SANDPLAIN

Peg Site*	Frequency (%)										
	0–50 μ	50–100 μ	100–150 μ	150–200 μ	200–250 μ	250–300 μ	300–350 μ	350–400 μ	400–450 μ	450–500 μ	<150 μ
1	2·0	10·5	22·5	56·5	4·5	2·0	1·0	0·5	0·3	0·1	35·0
2	2·0	10·5	17·5	57·5	6·5	2·5	2·0	1·0	0·5	0·4	30·0
3	3·5	15·0	64·5	11·5	3·5	1·9	1·0	0·1			83·0
4	6·0	17·5	47·5	26·0	2·9	0·1					71·0
5	3·0	15·0	50·0	30·0	1·0	0·5	0·4	0·1			68·0
6	2·0	12·0	31·0	45·0	5·5	3·0	1·0	0·5	0·4	0·1	45·0
7	5·0	12·0	28·5	45·5	5·0	2·0	1·5	0·4	0·1		45·5
8	5·0	14·5	22·5	38·5	9·5	4·0	2·5	1·5	1·9	0·1	42·0
9	2·0	12·0	24·0	46·0	6·5	3·5	2·5	1·5	1·0	0·5	38·0

* The position of the peg sites is marked on the cross section a–b in Figure 1.

(b) *Moisture Patterns*

(i) *Rainfall.*—An obstruction the height of the average dune in the path of rain-bearing winds would be expected to cause wind turbulence with a corresponding effect on the incidence of rainfall. Standard 8-in. rain-gauges were established vertically

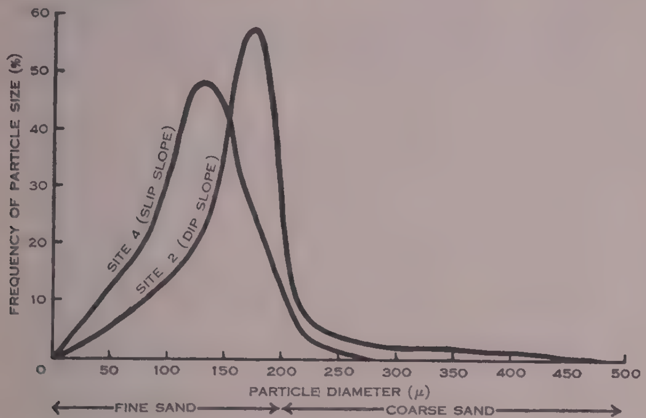

Fig. 13.—Frequency distribution curve of particle size for ½–1 in. sand samples taken on the dip and slip slopes of a dune.

in an east-west line over a recently burnt dune, at the sites marked on the cross section shown in Figure 14. The gauges were covered with a standard ¼-in. film of SAE 20 oil to prevent evaporation, and were read at monthly intervals.

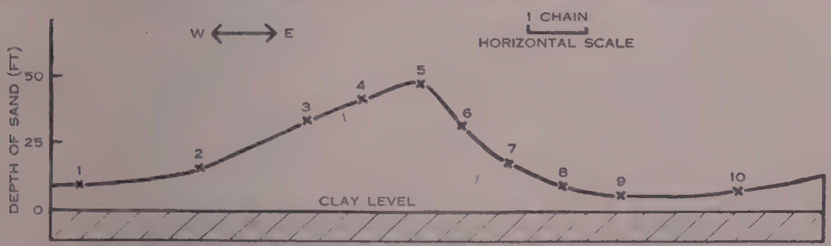

Fig. 14.—The cross section of a dune, showing the position of 10 standard 8-in. rain gauges. **The vertical scale is 3 times the horizontal scale.**

Rainfall recordings for 7 months are shown in Table 3. Readings at the dune crest were consistently low. With westerly winds, the rainfall incidence is lowest on western-facing slopes and highest on the dune slip face and the sandplain, an opposite effect to the rain-shadow created by mountain ranges. The average total rainfall over the period July 1954 to February 1955 was 10·80 in. for the western slope, and 11·52 in. for the eastern slope and sandplain. Translating this difference in terms of the average annual rainfall for this area, if sandplain and eastern aspect received 18 in. p.a., west-facing slopes would receive only 16¾ in. p.a. The rainfall pattern was reversed in October 1954 and February 1955 (see Table 3), when the

TABLE 3

RAINFALL RECORDINGS OVER A 7-MONTH PERIOD FROM JULY 1954 TO FEBRUARY 1955 FROM 10 STANDARD 8-IN. RAIN GAUGES ESTABLISHED IN AN EAST-WEST LINE OVER A DUNE IN THE SITES MARKED IN FIGURE 14

Date	Rainfall (in.)									
	1	2	3	4	5	6	7	8	9	10
3.vii.54	*	1·39†	1·36†	1·37†	1·40†	1·44	1·44	1·46	1·44	1·43
25.vii.54	*	1·48†	1·41†	1·42†	1·43†	1·53	1·53	1·58	1·58	1·59
26.viii.54	*	0·80†	0·77†	0·77†	0·76†	0·83	0·86	0·87	0·92	0·89
25.ix.54	0·94	0·89†	0·84†	0·83†	0·82†	0·91	0·92	0·97	1·00	0·95
24.x.54‡	1·55	1·50	1·46	1·45	1·22†	1·36†	1·43†	1·47	1·56	1·51
23.xi.54	1·86	1·78†	1·74†	1·75†	1·74†	1·83	1·86	1·89	1·90	1·82
2.i.55	1·20	1·17†	1·14†	1·12†	1·13†	1·23	1·20	1·27	1·28	1·23
6.ii.55	0·15†	0·13†	0·14†	0·16†	0·17	0·17	0·19	0·20	0·20	0·18
17.ii.55‡	1·96	1·94	1·97	1·96	1·79†	1·85†	1·90†	1·94	1·96	1·99

* No record.
† Rain below the average of all sites, at any one time.
‡ Easterly winds; see Australian weather maps for 23.x.54 and 8–10.ii.55, issued by the Commonwealth Meteorological Branch.

greater part of the month's rainfall was derived from storms, which blew in from the east (see Australian weather maps for October 23, 1954 and February 8–10, 1955, issued by the Commonwealth Meteorological Branch). Such storms are relatively rare.

(ii) *Soil Moisture.*—Soil moisture samples were taken from peg sites 1–9, Figure 1, before and after an opening rain of 2·94 in. in April 1954. The soil moisture was determined gravimetrically. Samples taken in March 1954 showed that the soil was at or below wilting point (see Table 4). Following the rains, the depth of moisture

TABLE 4

PERCENTAGE SOIL MOISTURE, DEPTH OF MOISTURE PENETRATION, AND CALCULATED SOIL MOISTURE STORAGE FOR THE 9 SITES ON CROSS SECTION *a–b*, FIGURE 1

Peg Site	Plant Group	Moisture on 29.iii.54 (%)	Moisture on 26.iv.54 (%)	Moisture Penetration on 26.iv.54 (in.)	Soil Moisture Storage on 26.iv.54 (in.)
1	A+B+D	0·94	4·79	65	3·99
2	A+B+D	1·31	3·06	61	2·28
3	A+B+D	0·85	3·40	41	1·67
4	A+B+D	0·63	3·65	45	2·00
5	F	0·84	4·93	63	4·23
6	F	0·79	4·26	20	1·05*
7	C+G	0·67	4·11	27	1·30*
8	C+G	1·23	4·44	64 to clay	3·61
9	A, B+D	0·67	3·66	41	1·81

* Sites within the variable rain-shadow.

penetration was recorded as the samples were taken and the amount of rain (in.) stored in the soil (soil moisture storage) was calculated by the formula:

$$\frac{D.P. \times W \times Sp.G.}{100},$$

where $D.P.$ is the depth of penetration in inches, W the percentage of moisture, and $Sp.G.$ the apparent specific gravity. The results are shown in Table 4. There was some evidence for a rain-shadow effect in sites 6 and 7. Numerous auger borings, spaced at approximately 1-yd intervals, established the fact that shallow moisture penetration occurred in discontinuous patches varying from 10 to 25 yd in width at the base of the slip slope. Considering the irregularity of the pattern and the extensive horizontal root spread of many of the heath species, the effect is unlikely to exert much influence on plant distribution. The average soil moisture storage was 2·58 in. for plant groups C, G, and F, and 2·35 in. for groups A, B, and D. Again translating this in terms of the average annual rainfall, while the eastern aspect and sandplain (C, G, and F) received 18·0 in. p.a., west-facing slopes (A, B, and D) received approximately 16½ in. p.a. The calculations closely approximate the actual rainfall recorded in (i) above. A similar soil moisture survey was repeated on a slightly lower dune approximately ½ mile distant. Moisture penetration was almost uniform at 4 ft

throughout. The average percentage moisture was 3·75 in. for the eastern slope and 3·45 in. for the western slope. This ratio is of the order of 18 : 16 in. of rain p.a. There was no evidence of a rain-shadow at the base of the eastern slope.

(c) *Light*

The dune, Figure 1, was modelled to scale and examined under a solar-scope (Phillips 1950). For each month of the year the total daily sunlight and the ratio of morning to afternoon sunlight were recorded for every 1-sq. ch quadrat on the model. The average hours of sunlight per day and the average ratio afternoon : total sunlight were calculated for each quadrat.

The data was grouped according to the vegetation communities A+B+D+E, C+G, and F (Table 5), and an analysis of variance carried out. There was no significant difference between the hours of sunlight falling on groups A+B+D+E and C+G, but both were significantly different ($P<0 \cdot 1$) from community F.

Table 5

THE AVERAGE DAILY HOURS OF SUNLIGHT AND THE RATIO OF AFTERNOON TO TOTAL SUNLIGHT FOR THREE PLANT COMMUNITIES

Plant Group	A+B+D+E	C+G	F
Average daily hours of sunlight	11·2	11·1	10·45
Afternoon : total sunlight ratio	0·55	0·46	0·40

Evaporation and transpiration rates will be affected by the differences in total daily insolation between habitats. When dew is present morning sunlight will cause its evaporation, while the afternoon sunlight will directly influence soil temperature. Western slopes are therefore subjected to the severest drying conditions.

The longer daily hours of total and afternoon sunlight will result in closer values for maximum day and minimum night soil temperatures on the western slopes. Using tomato and chili pepper, Went (1945) and Dorland and Went (1947) have shown that stem elongation and leaf area were increased by alternation of high day and low night temperatures, owing to the fact that the temperature optimum for photosynthesis is higher than that for the translocation of the products of photosynthesis. The difference in day and night temperatures required to produce optimal growth conditions depended on the species employed and the age of the plants. It is possible that on the western dune slopes suboptimal temperatures for translocation in combination with poorer moisture conditions may limit the growth rate of plants in this habitat.

V. Discussion

The heath vegetation of the upper south east of South Australia is not homogeneous in composition but can be separated into four plant communities by an objective method of vegetation classification. Three of these communities were logically delimited by differences in microhabitat which depend on the essentially

unidirectional rain-bearing winds and on the dune topography. The microhabitats can be described in terms of soil character and microclimate as follows:

(i) Eastern dune slopes, which combine soil of higher water-retaining capacity, a high incidence of rainfall, shorter average daily hours of sunlight, and a low afternoon : total sunlight ratio.

(ii) Western dune slopes, which combine coarser sands, low rainfall incidence, longer average daily hours of sunlight, and a high afternoon : total sunlight ratio.

(iii) The sandplain, which has similar rainfall incidence to the eastern slopes, similar average daily hours of sunlight to the western slopes, and soil texture and afternoon : total sunlight ratio intermediate between those of eastern and western slopes.

The eastern dune slope communities can be expected to contain more mesic elements of the flora, the western slope community species adapted to drier conditions, and the sandplain community elements common to both. This is in fact expressed to some degree by both the individual densities of species (Figs. 2–11) and by percentage frequencies of species (Table 1). However, both methods of summarizing the vegetation pattern are inadequate. Considering *B. ornata*, neither the density of 17–18 plants per chain (Fig. 3) nor the frequency of 90 per cent. in quadrats on the western slopes (Table 1) gave any indication of the slower growth rate of plants in this position.

A discrepancy between the observed and expected plant distributions also occurred in the case of species, such as *L. coriaceum* which were found on both eastern and western aspects of the dunes, but were completely absent from the sandplain. The explanation for this probably lies in the instability of the dunes. Successive layers of sand and ash found in auger borings on the eastern dune slopes showed that dune drift towards the east occurs, especially following periodic devegetation by burning. Plants which are both perennial and resistant to fire, as is the case with most heath species, though originally established on the eastern slope could be gradually transferred to the dune crest and finally to the western aspect by the sand movement, and there persist in a stunted form.

A gentle gradation of minor changes in soil, moisture, and light determine the differences in microhabitat, and, though these have been conveniently summarized in terms of means, there were no clear-cut boundaries to the habitats. Similarly, the statistically determined communities are artificial groupings of species and species frequencies. The concept of a varying continuum, advanced by Goodall (1953), fits the facts more closely. Figures 2–11 show that the density maxima of individual species rarely coincide and certainly do not fall into readily distinguishable groups. The character of the continuum therefore depends primarily on the individual growth tolerances of the species. Vegetation of the eastern dune slopes was characterized by the only tree species found in heath, by species common to the mallee-heath and mallee-broombush associations, and by low densities of *C. pusilla* and *X. australis*, both co-dominants of the heath association as a whole (Coaldrake 1951). It is therefore probable that interspecific competition for more favourable growth sites is a secondary influence in determining variation in the continuum.

VI. Acknowledgments

The author is indebted to Professor J. G. Wood, Dr. R. L. Specht, and Mr. B. Mason for advice and criticism during this work. The Adelaide Meteorological Bureau and the Commonwealth Department of Works assisted with the loan of equipment. Miss Leonie Sherwood helped in the preparation of the maps.

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DARK ISLAND HEATH (NINETY-MILE PLAIN, SOUTH AUSTRALIA)

III. THE ROOT SYSTEMS

By R. L. Specht* and Patricia Rayson*

[*Manuscript received February* 28, 1957]

Summary

This paper describes the nature of the root systems of the most important members of the heath community. Several variations of tap-root and fibrous root systems were observed. Tap-rooted species were either shallow rooting (1–2 ft) or deep rooting (6 or more feet into the clay subsoil). Two variations of deep tap-rooted species were observed. The tap-root of one decays with age; the laterals of the other produce frequent sucker shoots. In all forms of the deep tap-rooted species an extensive lateral root system was developed within the surface 12 in. of soil—the organic A_1 horizon; the tap-root and occasional secondary vertical descended, often unbranched, to the subsoil. The fibrous root system may arise from stem bases, rhizomes, tubers, or underground stocks (caudices). With the exception of underground stocks, which had extensive roots in the A_2 and A_3 to B horizons, the other forms of the fibrous root systems were confined to the A_1 horizon.

The marked concentration of roots in the organic A_1 horizon was illustrated in dry weight depth curves. Most of the roots in the A_2 and A_3 horizons arose from the caudex of *Xanthorrhoea australis* R.Br.; the remainder were vertical roots which passed directly into the subsoil from the deep-rooted species.

About 70 per cent of the species recorded in the heath had morphological characteristics which enabled them to survive a fire and sprout from perennating buds buried under the surface of the ground. Thus, although the aerial organs of the heath were destroyed by fire, the root systems provided a reserve of food and nutrients for the regenerating heath. The dry weight of the root systems was therefore scarcely influenced by fire and thereafter steadily increased in the organic A_1 horizon as the stand aged.

The presence of root nodules on species of Leguminosae and Casuarinaceae as well as of haustoria on *Exocarpos sparteus* R.Br. and *Euphrasia collina* R.Br. is recorded.

I. Introduction

In the first paper of this series (Specht and Rayson 1957) the general characteristics of the climate, soils, and vegetation of the ecosystem were described. Fires are an important factor in the ecosystem. In the present paper the root systems of the most important members of the heath community were studied in order to define their zones of greatest activity within the soil and their ability to survive the effect of fires.

II. Methods

(*a*) *The Individual Root Systems*

The technique of carefully picking out or washing out root systems from the face of a pit (Weaver 1926) was found useless for the investigation of the root systems

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of the larger species in the heath community. As will be shown in Section III, their horizontal surface roots depart from the tap-root in many directions and then branch so frequently that it was impossible to obtain a true picture of their distribution from the single plane presented by the face of a pit. It was necessaary to remove carefully the sandy soil from around the base of the plant and trace roots through the soil in all directions. An investigation of several plants of each species enabled reconstruction of the root systems in both horizontal and vertical planes. Unfortunately the depth and hardness of the clay subsoil prevented detailed examination of root systems in this horizon.

The smaller plants were investigated by removing the entire root system in a block of soil and then mapping the roots as they were disentangled from the sand.

(*b*) *Root Density*

An area 4 ft square was chosen at random in each of three stands of heath which had been fired, 3, 9, and 25 years previously. The vegetation on these areas was mapped at the end of the summer season, when soil moisture was at its lowest level (Specht 1953). Successive 3-, 6-, or 12-in. layers of soil were removed from each area. Each layer was sieved to remove all root material, which was then dried at 95°C to constant weight.

The density of the root systems in the 9-year stand was examined in greatest detail. The roots from successive 3-in. layers of soil were collected down to a depth of 24 in. Two layers of 6 in. each were sieved between the 24- and 36-in. depth, and beyond that depth layers of 12 in. were examined down to the B horizon of clay at 68 in. In the light of results obtained from the 9-year stand of heath, the densities of the root systems under the other two stands were investigated to a depth of only 30 in. Two 3-in. layers were taken from between the 0- and 6-in. depth; below that depth, 6-in. layers were examined.

From the point of view of statistics a single sample from under each stand of heath cannot be regarded as sufficient, but the labour and time involved prevented further replication. As counts of the species present on the areas indicated that the vegetation was representative of each stand, it was assumed that the data on these root systems were representative of the stands as a whole.

The roots, stocks, and leaf bases of *Xanthorrhoea australis** were hand-separated from underground organs of other species in the 9-year stand. It was impossible to identify finer roots in the samples, but separation of the major root material enabled a reasonable estimate to be made of the percentage contribution of *Xanthorrhoea* to the underground material at any depth.

III. Results

(*a*) *The Individual Root Systems*

The root systems of the 91 species of the heath community may be conveniently grouped under two broad categories: (i) species which possess tap-roots,

* Nomenclature follows that used in part I of this series (Specht and Rayson 1957, Appendix I).

and (ii) species which possess a fibrous root system. Within each category, however, there are several subdivisions based on peculiarities of the particular root system. Examples are set out below.

(i) *Species which Possess a Tap-root.* (1) *Deep Tap-root. Normal Form*: Banksia ornata *Type* (*Figs.* 1, 2, *and* 4).—Many of the larger species of the heath possessed a tap-root which penetrated deeply into the subsoil clay. There, the

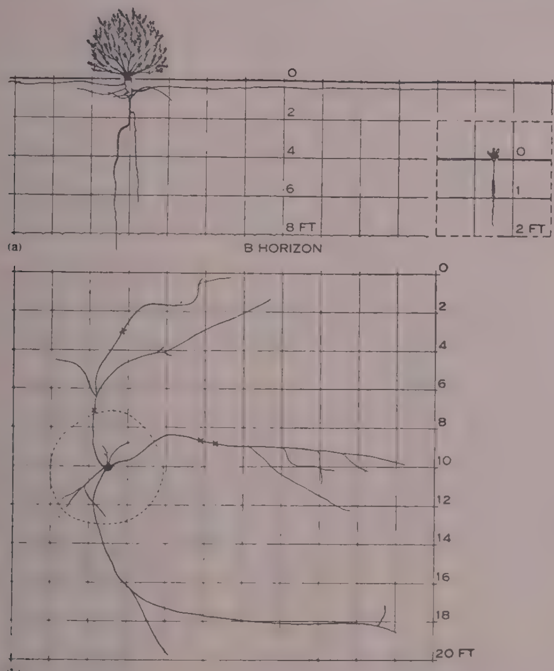

Fig. 1.—Root systems of *Banksia ornata* in the Makin sand as seen in a vertical plane (*a*) and in a horizontal plane within 3–9 in. of the surface (*b*). The crosses in the lower diagram indicate the position of secondary vertical roots. The inset in (*a*) shows the root system of a 4-months-old seedling of this species. The root system of this species is typical of the deep tap-root form.

tap-root divided into fine roots which penetrated every crack in the clay. Much of the root system, however, was confined to the upper 10–12 in. of soil (the A_1 organic horizon), where an extensive system of horizontal, lateral roots occurred. These lateral roots branched and re-branched over a considerable area in comparison with the size of the plant. From them, roots arose at irregular intervals and descended vertically into the clay; these roots were usually much smaller in diameter than the tap-root. The deep tap-root system was apparent even in seedlings which showed a strongly developed tap-root in comparison with the development of the lateral roots.

(2) *Deep Tap-root which Decays with Age*: Casuarina pusilla *Type* (*Fig.* 3).—The root system of this group developed as in the normal form, but eventually the original tap-root decayed near the departure of a lateral root some 9–12 in. below the surface of the soil. Even this lateral root may decay about 12 in. from its point of departure. The root system then consisted of a massive, central L-shaped root from which the horizontal lateral roots departed. The secondary vertical roots from these horizontal roots take over the function of the original tap-root.

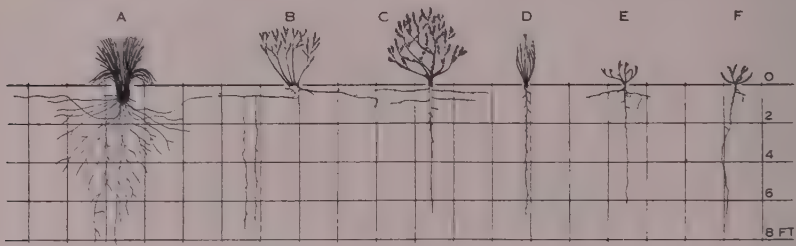

Fig. 2.—Root systems of *A*, *Xanthorrhoea australis*; *B*, *Leptospermum myrsinoides*; *C*, *Casuarina muelleriana*; *D*, *Loudonia behrii*; *E*, *Spyridium subochreatum*; and *F*, *Daviesia brevifolia* as seen in a vertical plane in the Makin sand. *A* is typical of the fibrous roots arising from a stock; all the other species have deep tap-rooted forms.

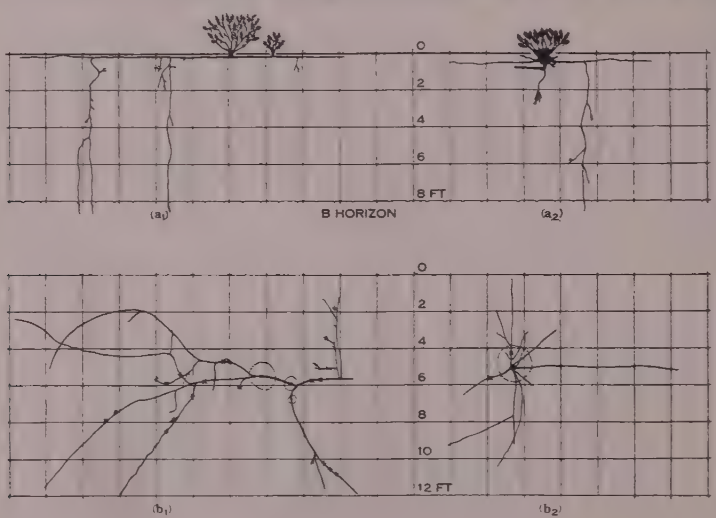

Fig. 3.—Root systems of *Banksia marginata*, (a_1) and (b_1), and *Casuarina pusilla*, (a_2) and (b_2), as seen in a vertical plane and a horizontal plane within the organic A_1 horizon (9–12 in. deep). The crosses in (b_1) and (b_2) indicate the position of secondary vertical roots. The root system of *Banksia marginata* is typical of the deep tap-rooted form with suckers developing from the lateral roots; that of *Casuarina pusilla* is typical of the deep tap-rooted form whose tap-root decays with age.

(3) *Deep Tap-root with Suckers Developing from the Lateral Roots*: Banksia marginata *Type* (*Figs.* 3 *and* 4).—The root system of this group developed as in the normal form, but possessed in addition an extensive horizontal, lateral root system 3–6 in. below the surface. Early in winter, portions of the horizontal root system about 1 ft long thickened and produced numerous vegetative buds. Only

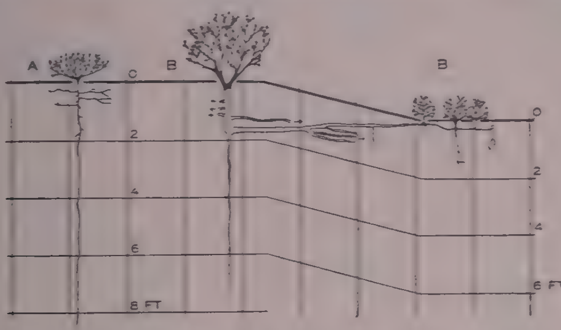

Fig. 4.—Root systems of the two species of *Phyllota* as seen in a vertical plane in the Makin sand. *A, P. remota,* is a normal deep tap-rooted form; *B, P. pleurandroides,* is a tap-rooted form which produces suckers from the lateral roots.

a few of the buds developed to produce sucker shoots, all attached to the root system of the parent plant. With increased metabolic activity of the aerial system, the secondary vertical roots increased in size, and the area of exploitation of the shallow, horizontal roots was increased. Eventually it was often impossible to distinguish the parent plant, which sometimes decayed.

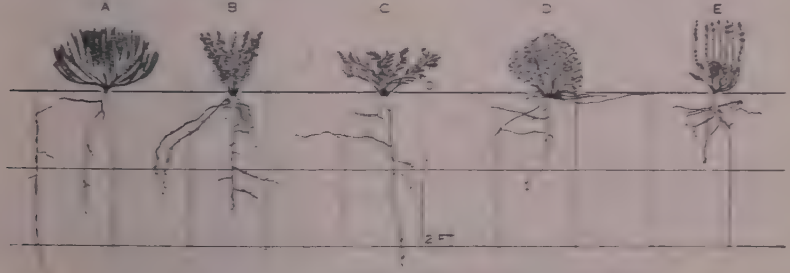

Fig. 5.—Root systems of *A, Hibbertia stricta*; *B, Hibbertia sericea*; *C, Calytrix alpestris*; *D, Cryptandra tomentosa*; and *E, Euphrasia collina* as seen in a vertical plane in the Makin sand. All these root systems are typically shallow tap-rooted forms.

(4) *Shallow Tap-root*: Leucopogon costatus *Type* (*Figs.* 5, 6, 7, 8*A*, *and* 9*A*).—Many of the smaller perennial species of the heath were found in this sub-category. The tap-root developed but lateral roots were almost as prominent. Both sets of roots branched repeatedly over a short distance, so that a dense mass of roots was formed in a volume of soil not more than 2–3 times the diameter of the aerial portion

of the plant and frequently not more than 12 in. in depth. Sometimes roots penetrated beyond the A_1 horizon to a depth of up to 24 in. but this was exceptional.

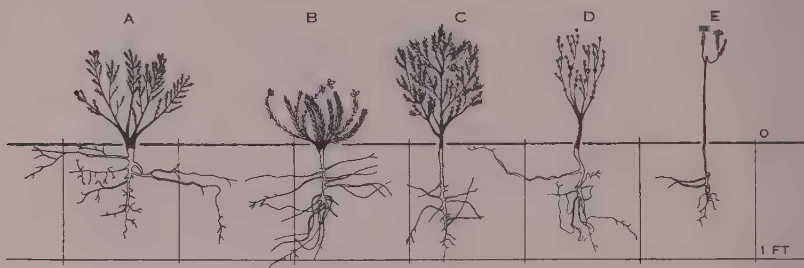

Fig. 6.—Typical root systems of *A*, *Boronia caerulescens*; *B*, *Gompholobium minus*; *C*, *Leucopogon woodsii*; *D*, *Leucopogon costatus*; and *E*, *Pimelea octophylla* as seen in a vertical plane in the Makin sand. All these root systems are typically shallow tap-rooted forms.

(ii) *Species which Possess a Fibrous Root System.* (1) *Fibrous grass roots*: Stipa semibarbata *Type* (*Fig.* 8).—A dense mass of slender, branching roots of about equal size arose from the hypocotyl region of the plant. These roots did not penetrate beyond the A_1 horizon.

(2) *Rhizome with Fibrous Roots*: Hypolaena fastigiata *Type* (*Figs.* 8 and 9*D*).—These species possessed a well-marked rhizome from which a fibrous root system arose.

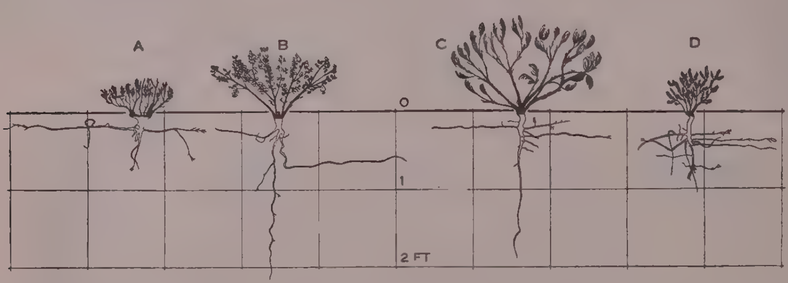

Fig. 7.—Root systems of *A*, *Astroloma conostephioides*; *B*, *Correa rubra*; *C*, *Adenanthos terminalis*; and *D*, *Dillwynia hispida* as seen in a vertical plane in the Makin sand. All species except *A. terminalis* are typical of the shallow tap-rooted forms. The tap-root of *Adenanthos* extends at least to the clay.

(3) *Tuber with Fibrous Roots*: Lyperanthus nigricans *Type* (*Fig.* 9*B*).—These species possessed tubers from which a fibrous root system arose.

(4) *Stock with Fibrous Roots*: Xanthorrhoea australis *Type* (*Fig.* 2*A*).—*X. australis* was an unusual species in the heath, for its adventitious root system arose from a deeply seated rootstock (caudex). This stock was frequently 9–12 in. below the surface, but sometimes deeper (15–18 in.) on the sand ridges. The stock sometimes branched several times to produce several crowns of leaves from the same root system. The green leaves of this species arose from the centre of this

stock and were surrounded by a thick layer of compressed fibrous, resinous remnants of the leaf bases of dead leaves which were very resistant to decomposition. The

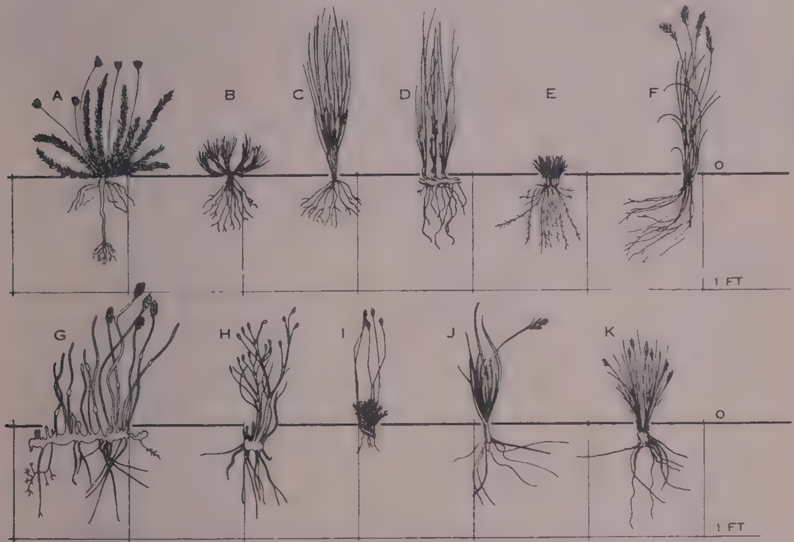

Fig. 8.—Root systems of *A*, *Olearia ciliata*; *B*, *Lomandra glauca*; *C*, *Lomandra leucocephala*; *D*, *Lomandra juncea*; *E*, *Schoenus tepperi*; *F*, *Stipa semibarbata*; *G*, *Lepidobolus drapetocoleus*; *H*, *Hypolaena fastigiata*; *I*, *Amphipogon caricinus*; *J*, *Lepidosperma laterale*; and *K*, *Lepidosperma carphoides* as seen in a vertical plane in the Makin sand. Apart from *A*, a shallow tap-rooted form, all the other species possess typical fibrous roots which arise from either stem bases or rhizomes.

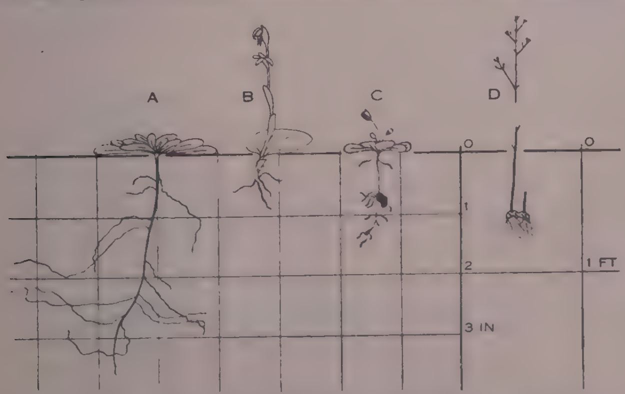

Fig. 9.—Root systems of *A*, *Goodenia geniculata*; *B*, *Lyperanthus nigricans*; *C*, *Drosera whittakeri*; and *D*, *Thysanotus dichotomus* as seen in a vertical plane in the Makin sand. Shallow tap-roots are shown in *A* and *C*, fibrous roots from a tuber in *B*, and fibrous roots from a rhizome in *D*.

diameter of the stock and the leaf bases varied from 3 in. to a maximum of 12 in. The size must depend upon the age of the plant. A mass of long, little-branched,

fibrous roots, which were covered by a loose, black sheath, emerged from the rootstock to explore much of the soil profile below the A_1 horizon.

The percentage of species which fall into each root type is indicated in Table 1. A quarter of the species possessed deep tap-roots, mostly normal in structure; about one-half of the species possessed a shallow tap-rooted system; the remaining quarter possessed fibrous roots.

Table 1

PERCENTAGE OF SPECIES OF THE HEATH VEGETATION WHICH POSSESS A PARTICULAR TYPE OF ROOT SYSTEM

Deep Root System			Shallow Tap-root	Fibrous Root System			
Normal	Decays	Suckers		Grass	Rhizome	Tuber	Stock
23	2	2	42	13	9	8	1

(b) *Root Density*

It will be clear from the above descriptions that much of the root systems was located in the upper 12 in. of the soil. Apart from that of *X. australis*, little of the root systems occurred in the A_2 and A_3 horizons (i.e. from 12 in. below the surface to the clay subsoil). In the subsoil an extensive network of fine roots occurred.

Figure 10 shows the dry weight of the underground organs per acre found in successive 3-in. depths of soil. The dry weight of underground organs per acre was high in the 0–3 in. depth, reached a maximum in the 3–6 in. depth, then fell rapidly through the 6–9 in. and 9–12 in. depths until it reached almost a constant minimum value from a depth of 2 ft downwards to the subsoil. In the A_1 horizon about 21,500 kg of dry matter per acre were found under a 9-year stand of heath. In contrast, the 56 in. of the A_2 and A_3 horizons (12–68 in. depth) contained only 5500 kg. of dry matter per acre.

Figure 11 illustrates the relative importance of *X. australis* in the three A horizons. The rootstock and leaf bases contributed 16 per cent. to the dry weight of the A_1 horizon, though these organs were not physiologically active in absorbing water and nutrients from the soil. *Xanthorrhoea* roots predominated in the A_2 and A_3 horizons, exploiting the soil which is of little importance to other species of heath except as a medium by which the roots of some may reach the more fertile B horizon.

IV. The Influence of Fire on the Root System

The effect of fires on the composition and structure of the heath vegetation will be discussed in a later paper of this series; in the present paper the ability of the various root systems to survive fire is indicated.

Beadle (1940) has indicated the range of temperatures within the soil when the heath vegetation growing on it is burnt. He found that the maximal temperatures,

though high on the surface of the soil, fell rapidly with depth. The position of the perennating buds in relation to the zones of combustion or high soil temperatures was crucial to the survival of the species. Beadle found that only those species which possessed either epicormic buds or ligno-tubers were able to survive fires which razed sclerophyll forest communities on the Hawkesbury sandstone area of New South Wales. Apart from scattered clumps of *Eucalyptus baxteri*, which possessed epicormic buds on their trunks and branches, no species of the heath at Dark Island possessed either of these two structures, yet a large percentage of the plants were able to survive a fire.

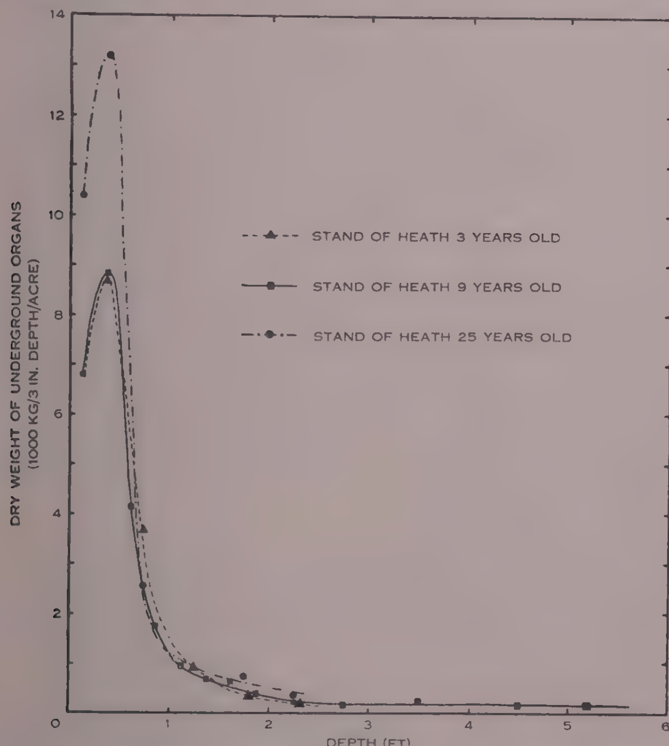

Fig. 10.—Graphs of the distribution of underground organs, as recorded in 3-, 9-, and 25-year-old stands of heath, expressed on a dry weight basis against depth in the Makin sand.

All species which possessed fibrous root systems had perennating buds buried to some depth in the soil. Hence, although aerial organs were destroyed, most of these species were able to survive fire and regenerate after the first rains.

Sixty-eight per cent. of the species which possessed a deep tap-root had perennating buds below the surface as well as on the aerial organs and were able to survive fire. Many branches arose from these buds and acted as a centre for accumulation of drifting sand, providing a further protection. The suckering, horizontal root system of *B. marginata* and *Phyllota pleurandroides* enabled them to survive a fire.

Four species of deep tap-rooted plants of the heath, *B. ornata*, *Phyllota remota* and two rare *Hakea* spp., had no underground perennating buds and were almost invariably destroyed by fire. Also, 60 per cent. of the species with shallow tap-roots had no underground perennating buds and were consequently destroyed by a fire, but species with their lower branches partially buried by mounds of sand, viz. *Hibbertia stricta*, *Hibbertia sericea*, *Cryptandra tomentosa*, *Correa rubra*, *Astroloma conostephioides*, *Astroloma humifusum*, *Acrotriche affinis*, and *Boronia caerulescens*, were able to survive.

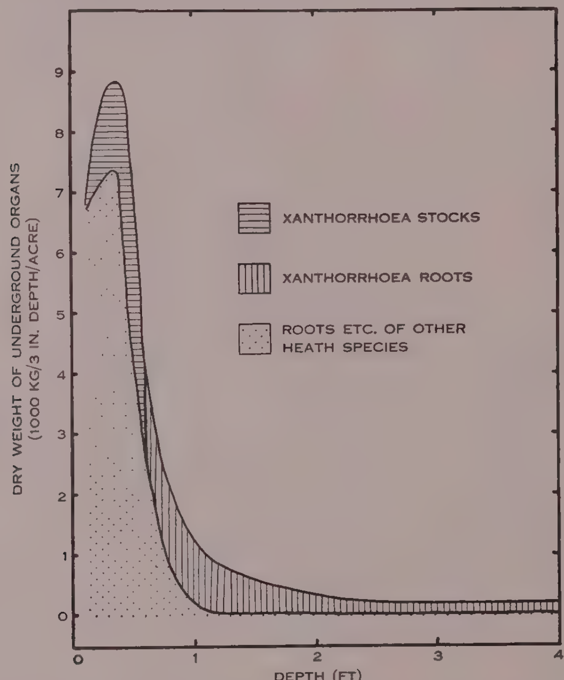

Fig. 11.—Graph of the distribution of underground organs, expressed on a dry weight basis, against depth in the Makin sand as recorded in a 9-year-old stand of heath. The proportion which *Xanthorrhoea australis* contributes to the underground organs is illustrated.

Almost 70 per cent. of the species present within the heath vegetation were able to survive a fire and regenerate using reserves of food material stored in their underground organs.

Immediately after a fire, the underground material is composed of a large mass of living roots of "razed species" and a smaller mass of dead roots of the destroyed species. To this will be added the fine roots of the seedlings which will, in time, compensate for the dead roots which are slowly decomposing. It was not surprising, therefore, that, when a stand of heath 6 years old was burnt, the resultant

mass of underground material was almost the same as that of the unburnt stand when both were examined 3 years later (Fig. 10).

With increasing age the underground organs of all the regenerating species slowly increased in size. Although root competition reduced the numbers of each species present within the stand, the mass of underground material continually accumulated until, 25 years after a fire, about 28,500 kg of dry matter was present in the A_1 horizon. In comparison with this, 21,500 kg was present under a 9-year stand. Much of this increase was concentrated in the upper 6 in. of soil (Fig. 10).

V. Root Nodules

(a) *Leguminosae*

Nodules have been observed occasionally on the roots of seedlings and on the fine roots of the older plants of all the Leguminosae present. The bacteria associated with them are apparently all capable of fixing atmospheric nitrogen (J. Harris, personal communication).

(b) *Casuarinaceae*

"Coralloid" masses, called nodules, have been observed occasionally on the fine rootlets of the species of *Casuarina* which were prominent within the heath. McLuckie (1923), working on *Casuarina cunninghamiana*, considered that bacteria associated with them were capable of fixing atmospheric nitrogen. However, some doubt has been cast on their importance by the work of Chaudhuri (1931) who was unable to show any significant difference between the growth of specimens of *Casuarina equisetifolia* which had bacterial nodules and of those which lacked them.

VI. Root Parasitism

Euphrasia collina was a consistent, but not prominent, member of the heath vegetation. Haustorial connections have been noted between the fine lateral roots of this species and those of *Hibbertia stricta* and of sedges. The haustoria did not seem to be numerous, but, as the roots were easily broken, may be more frequent than observed.

Exocarpos sparteus was occasionally found on the lee face of the major sand dunes of the area.

VII. Discussion

Most of the root systems of the heath vegetation on deep sands in the Ninety-Mile Plain were confined to the upper 10–12 in. of the soil—the organic A_1 horizon. Microbial activity is also at its maximum here (Loutit 1953). Except in the case of *X. australis*, little of the root systems occurred in the A_2 and A_3 horizons, but in the clay subsoil an extensive network of fine roots occurred.

During the long, dry summer periods, the root hairs of the surface root systems of all species sloughed off, leaving these portions non-functional. The subsoil portion of the deep root systems then became very active in moisture absorption. In spite of the long periods when the surface soil fell below wilting point (Specht 1953),

the shallow tap-rooted and fibrous-rooted species rarely died, although they sometimes became yellow and defoliated. Their water economy is not clear but dew may be important. When sufficient rain fell to moisten the A_1 horizon, development of root hairs was initiated and the horizontal root systems became functional. Frequently a dense mat of root hairs penetrated the moist decomposing litter (A_0 horizon).

The B horizon, although very poor in plant nutrients, is much higher in fertility than the sand above it. The deep tap-root and secondary vertical root systems were able to exploit this horizon and transport nutrients into their aerial portions. The nutrients will eventually return to the A horizon, either by way of leaf litter or as ash after a fire. Here they will re-enter the nutrient cycle of the system through the many shallow-rooted species. The root system of *Xanthorrhoea* explored the very infertile A_2 and A_3 horizons (Fig. 11). It will be shown in a later paper that very low amounts of nutrients occur within all organs in this species.

In the light of the nutrient cycle and the moisture regime, it is not surprising that the ecosystem favoured those species with a shallow root system supplemented by a deep vertical root system. In a sense the shallow-rooted species are "semi-parasites", since they rely almost entirely on the deep-rooted species for sufficient concentrations of many nutrients.

VIII. Acknowledgment

The authors wish to thank Miss Leonie Sherwood for preparing the diagrams for publication.

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FLORAL HISTOGENESIS IN THE MONOCOTYLEDONS

II. THE CYPERACEAE

By C. Barnard*

[*Manuscript received April 23, 1957*]

Summary

An account is presented of floral histogenesis in *Scirpus validus* Vahl, *Cyperus eragrostis* Lam., and *Carex appressa* R. Br.

The cells of the apex of the spikelet in the three species are arranged in a two-layered tunica over a central corpus. Histogenetically the outer and inner tunica layers behave differently and are termed dermatogen and hypodermis respectively. The same three tissue zones are recognized in the flower primordia.

Periclinal division of dermatogen and hypodermal cells gives rise to

(i) the glumes or floral bracts and carpels in all species,

(ii) the perianth members in *Scirpus*, and

(iii) the perigynium in *Carex*.

These are all classified as foliar organs.

Periclinal divisions in cells of the outer corpus layers, and inclined and periclinal divisions in the hypodermis, characterize the formation of flower and stamen primordia. Periclinal division of dermatogen cells never occurs. These organs are regarded as cauline.

The ovule develops directly from the growing point of the flower primordium and its integuments arise in the foliar fashion.

The general pattern of histogenesis is compared with that in the Gramineae. Variations within this pattern and the interpretation of the floral structures are discussed.

I. Introduction

The literature covering the histology of floral organogenesis has been reviewed by Joshi (1947) and more recently, though briefly, discussed by Barnard (1955, 1957). The few studies of the histogenesis of floral organs which have been made have dealt mainly with dicotyledons.

In the monocotyledons studies have so far been confined to the Gramineae. Holt (1954, 1955) studied *Phalaris arundinacea* L., *Dactylis glomerata* L., and *Avena* sp.; Barnard (1955, 1957) examined *Triticum aestivum* L. and six other grasses. Barnard (1957) concluded that the floral structures in the Gramineae could be classified according to their mode of origin as either cauline or foliar. Inflorescence branches, spikelets, flower primordia, and stamens belonged to the cauline group, whilst glumes, lemmas, paleas, lodicules, and carpels belonged to the foliar group. The flower was interpreted as a reduced branch system subtended by the lemma; the palea and lodicules as foliar structures upon its main axis; the stamens as reduced lateral branches bearing microsporangia; the gynaeceum as consisting of fused foliar structures upon the distal portion of the main axis; and the ovule as cauline in origin and not carpel-borne. These findings were not in accord with the classical concept of the morphological nature of the flower.

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In the present communication further studies on the monocotyledons are reported. The histology of floral organogenesis in three species of the Cyperaceae is described and the interpretation of floral structures in this family discussed in the light of the results.

II. Materials and Methods

The three species studied were: *Scirpus validus* Vahl (tribe Scirpeae); *Cyperus eragrostis* Lam. (tribe Cypereae) and *Carex appressa* R. Br. (tribe Cariceae).

Material of the three species was collected from plants growing in the field at Canberra. All stages of inflorescence and flower development were present in material of *Carex* collected during August, of *Scirpus* collected during November, and of *Cyperus* collected during December. After fixing in formalin-acetic-alcohol and evacuating all air from the tissues, material was stained in acid fuchsin in 95 per cent. alcohol. Dissection in absolute alcohol under the stereo-microscope permitted observations on the general floral morphology and ontogeny and enabled the materials to be sorted into stages for sectioning.

Serial longitudinal and transverse sections made in paraffin wax at 7μ were stained in iron alum haemotoxylin with light green or erythrosin as a counterstain. Drawings of the sections were prepared by photographing the subject and tracing an enlarged image from the negative.

III. Scirpus validus

(*a*) *Morphology*

In *Scirpus validus* Vahl the inflorescence is an irregular umbellate panicle borne singly in an apparently terminal position and subtended by a bract. Some 25 flowers are developed per spikelet although some of the distal ones fail to reach maturity. The glumes or bracts are imbricate in a close spiral on the rachilla and each subtends a flower. The perianth is in the form of six filiform and retrorsely barbellate bristles. There are three stamens, two lateral and one anterior; the ovary is one-celled with a single anatropous ovule and the style is bifid.

The general floral morphology and, in particular, the vascular anatomy of *Scirpus* and allied genera have been described by Snell (1936) and Blasser (1941*a*, 1941*b*). The perianth in *Scirpus* may be completely absent or represented by three to seven bristles or scales. Holttum (1948) reports that there are four to seven perianth members in *Scirpus littoralis* Schrad. and that they vary considerably in shape and size in different specimens. The stamens, though usually three, may be reduced to two or one. According to some observers the three stamens represent the outer of two whorls; others believe that one belongs to an outer whorl and two to an inner whorl. Holttum (1948) finds in *S. mucronatus* that the lateral stamens are not opposite the perianth bristles but between them. He concludes that it is "at least very unlikely that the three stamens represent a symmetrical whorl". The interpretation of the floral structure of *Scirpus* and allied genera based on an arrangement consisting of two perianth whorls and two whorls of stamens apparently needs confirming.

There is no doubt that in *Scirpus validus* the six perianth segments are arranged in two whorls and that each member of the outer whorl subtends one of the three stamens (Plate 1, Figs. 1 and 2). Thus of the latter, two are laterally and one is anteriorly placed. In their early stages of development the primordia of these "bristles" are flat. Two members of the inner whorl of the perianth are visible on the anterior side of the flower primordium. They arise between the anterior and lateral stamens and higher on the flower primordium than the members of the outer whorl (Plate 1, Fig. 1). The third member of the inner whorl is situated on the posterior side of the flower primordium and, therefore, between the two lateral stamens (Plate 1, Figs. 2 and 3). At the stage when the gynaeceum is arising the circle of carpellary tissue around the apex of the flower primordium has three very slight peaks. Each peak is opposite a stamen (Plate 1, Fig. 1). The three stamens thus represent a single outer whorl. The arrangement of flower parts therefore is symmetrical and of the liliaceous type, although the whole flower primordium is somewhat flattened in the antero-posterior plane.

(b) *Histogenesis*

The cells of the apex of the spikelet are organized into a two-layered tunica and a corpus (Fig. 1).

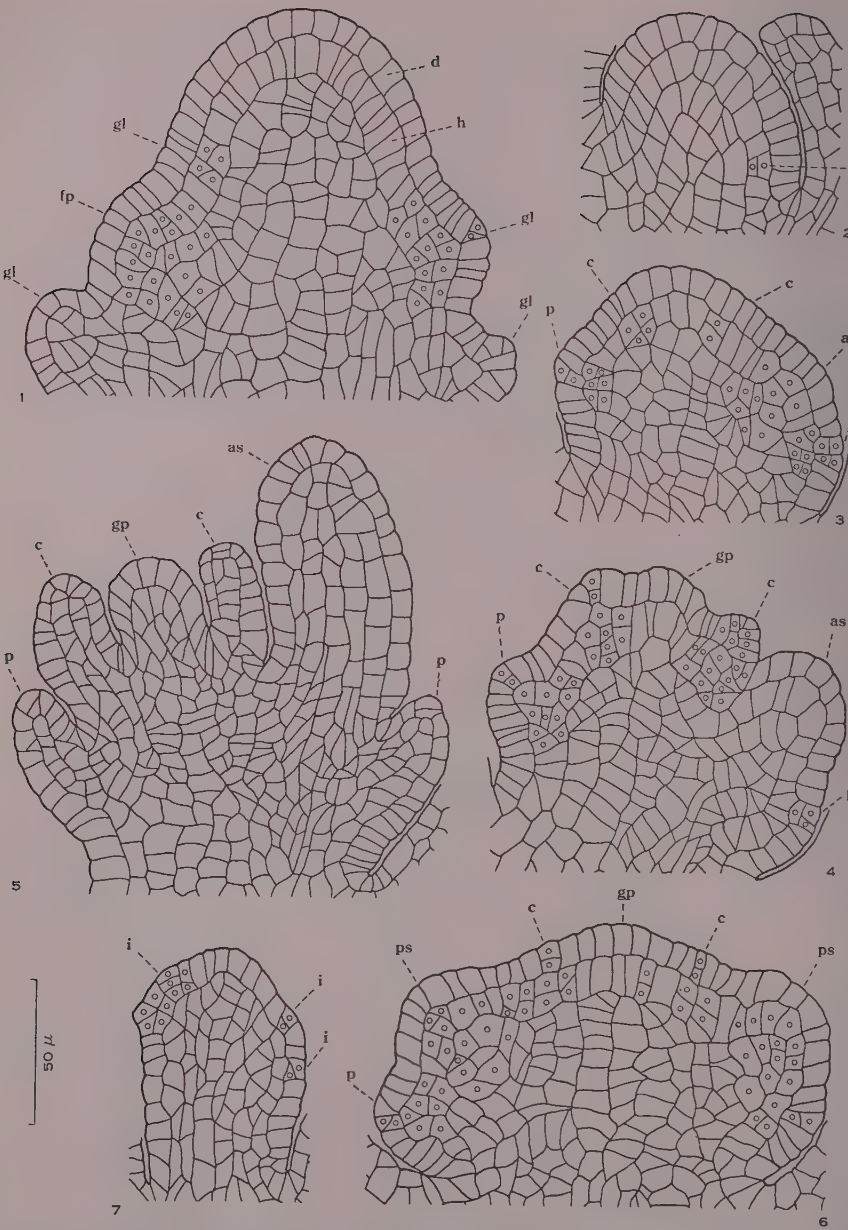
At the tip of the apex there is a polygonal apical cell similar to that occurring in the vegetative growing point in *Triticum* (Rösler 1930) and in *Avena* (Kleim 1937). The existence of this apical cell can be determined in transverse sections. Its derivatives divide only by anticlinal walls prior to the differentiation of glume primordia and constitute the dermatogen or outer layer of the tunica. In longitudinal section the cells of the dermatogen are rectangular.

The cells of the hypodermis or inner tunica layer are probably also derived from a single cell but this has not yet been definitely established. The cells of the hypodermis, like those of the dermatogen, divide only by anticlinal walls prior to the initiation of glume primordia. They are rectangular in shape in longitudinal section with the long axis in the direction at right angles to the surface. These characters clearly demarcate the cells of the hypodermis from those of the corpus.

The cells of the corpus also have their origin in either a single cell or a very small group of cells. In this zone cells divide in various directions though mainly in the direction at right angles to the axis of the spikelet. The cells of this area are thus arranged in short rows or files (Fig. 1). Vertical cell divisions increase the number of rows.

The glumes (or floral bracts) arise upon the apex in a spiral sequence (Plate 1, Fig. 1). The angular divergence, determined from serial transverse sections, varied considerably in one spikelet (from 70° to 180°) and in the average between spikelets (from 105° to 137°). This irregularity in phyllotaxis and the fact that successive glumes not only arise in close sequence but also overlap transversely made their histogenic origin difficult to determine.

The first indication of glume initiation is the periclinal division of hypodermal cells in the apex of the spikelet (Fig. 1). These divisions occur in a zone which extends



Figs. 1–7.—Sections of *Scirpus validus*. *d*, dermatogen; *h*, hypodermis; *gl*, glume; *fp*, flower primordium; *p*, perianth member; *as*, anterior stamen; *ls*, lateral stamen; *c*, carpel; *gp*, growing point of flower primordium; *i*, integument.

Fig. 1.—Longitudinal section of apex spikelet. Fig. 2.—Longitudinal section of very young flower primordium. Figs. 3–5.—Longitudinal section of older flower primordium. Fig. 6.—Tangential longitudinal section of flower primordium. Fig. 7.—Longitudinal section of very young ovule. In Figures 2–5 the axis of the spikelet is on the left.

transversely for a little over one-third of the circumference of the axis, and initially involve two to three cells in the vertical plane. Hypodermal cells above and below these then divide by periclinal walls until five or six cells in the vertical plane have divided. Following further subdivision of hypodermal cells towards the centre of the area of initiation the young glume primordium becomes evident as a crescentic bulge around the axis. Along the crest of this bulge, periclinal (and inclined) divisions occur in dermatogen cells (Fig. 1). Subsequent development of the primordium is the result of the continued division of these cells and derivatives of the hypodermal cells which initiated the primordium. Cells of the corpus in the region of glume differentiation may also divide periclinally. These cells do not contribute to the tissues of the glume. They become elongated and constitute part of the provascular strand in the axis which later becomes continuous with the provascular strand of the glume.

The flower primordia arise in the axils of the glumes. Periclinal divisions in cells of the hypodermis are followed by periclinal and inclined divisions in cells of the corpus (Fig. 1). It is probable that the inner cells resulting from the division of the original hypodermal cells undergo further periclinal divisions. The derivatives of these cells could not be distinguished from derivatives of the corpus and therefore the precise sequence of cell divisions which leads to the differentiation of the flower primordium was not determined. It is certain, however, that no periclinal divisions occur in the dermatogen, and that derivatives of corpus cells contribute to the tissue of the flower primordium.

Very early in the development of the flower primordium a definite hypodermis is organized (Fig. 2). Cells of this layer, prior to the initiation of the perianth, divide only by anticlinal walls. The cells of the inner tissue or corpus are at first arranged in regularly disposed files (Fig. 2) but as growth continues this regularity of arrangement becomes less evident (Fig. 3). It is clear that

(i) the dermatogen of the flower primordium is derived solely from the dermatogen of the axis;

(ii) the hypodermis of the flower primordium originates in the hypodermis of the axis, and

(iii) the corpus of the flower primordium is derived from both hypodermal and corpus cells of the axis.

Longitudinal sections of the spikelet which pass medianly through a flower primordium give median sections of both the anterior and posterior perianth members. Such sections are illustrated in Figures 2–5. The perianth members arise by the periclinal division of hypodermal cells followed by the periclinal division of dermatogen cells. The mode of origin of the perianth is thus similar to that of the glumes. The anterior perianth member is initiated prior to the posterior member (Fig. 2) and is morphologically lower on the axis of the flower primordium (Fig. 3).

The stamens and carpels arise almost simultaneously. The stamens arise in a manner comparable with that of the flower primordium; the carpels arise like the glume and the perianth. Figures 3 and 4 illustrate the origin of the anterior stamen; periclinal divisions occur in the hypodermis and periclinal and inclined divisions in the outer cells of the corpus. A distinct hypodermis is reconstituted

early in the development of the stamen primordium (Fig. 4) in the same way as in the flower primordium. No periclinal divisions occur in the dermatogen.

The carpellary tissue originates in periclinal divisions in the hypodermis (Fig. 3) followed by similar divisions in the dermatogen (Fig. 4). These divisions occur more or less simultaneously in a ring around the apex (Figs. 3–6), and give rise to a circular ridge. Growth of this ridge of carpellary tissue is apical and repeated divisions of derivatives of dermatogen cells contribute the bulk of its tissue. Just subsequent to the stage represented in Figure 5, growth becomes more rapid at three centres on the encircling ridge and three peaks are formed. One of these peaks is anteriorly and two are laterally placed (Plate 1, Fig. 1). Growth of the anteriorly placed peak subsequently ceases, but it continues at the two lateral peaks. Each of the lateral peaks develops into a branch of the style.

The growing point of the flower primordium continues to grow forward within the encircling carpels to become the ovule. The integuments arise principally, if not entirely, by periclinal divisions in the dermatogen (Fig. 7). As the integuments commence to differentiate, the growing point turns away from the axis of the spikelet and then downwards, so that the ovule when fully developed is anatropous. The megaspore mother cell forms a linear tetrad; the three micropylar megasphores degenerate and the chalazal one is functional. A group of densely cytoplasmic, elongated, and apparently secretory cells are formed on the abaxial side of the funiculus. These cells are immediately below the micropyle.

IV. Cyperus eragrostis

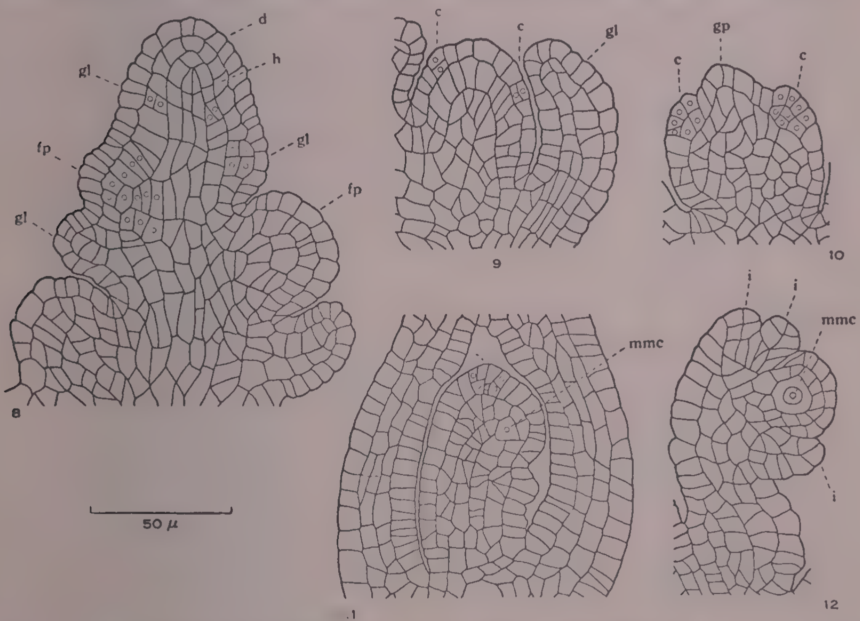
(*a*) *Morphology*

The inflorescence in *C. eragrostis* Lam. is umbellate with conspicuous leaf-like bracts subtending its branches. The spikelets are clustered at the ends of the branches of the umbel. The glumes are distichous and imbricate in two opposite rows, each glume subtending a flower. The number of flowers in each spikelet varies from 20 to 30. No perianth is developed. The flowers of this species are usually described as hermaphrodite but in the plants examined some of the flowers were unisexual. The unisexual flowers were always female and consisted of a gynaeceum only. The bisexual flowers were composed of gynaeceum and one lateral stamen. The number of bisexual and unisexual flowers varied among the spikelets, the former generally constituting about 30–40 per cent. of the total number. No correlation existed between the sex of a flower and its position on the spikelet. The ovary is one-celled with a single anatropous ovule. The style is trifid though sometimes the anteriorly placed branch is not very well developed.

(*b*) *Histogenesis*

The apex of the spikelet of *Cyperus* is less massive than that of *Scirpus* and the glumes arise alternately on opposite sides of the axis. However, organization of cells of the apex into a dermatogen, hypodermis, and corpus is similar to that in *Scirpus*. The glumes are initiated in the same way by periclinal division of hypodermal cells (Fig. 8). Periclinal division of dermatogen cells occurs also but not as frequeutly in the early stages of glume formation as in *Scirpus*.

The mode of initiation of the flower primordia is very similar to that described for species of the Gramineae (Barnard 1957). The first indication of flower primordium differentiation is the occurrence of periclinal divisions in a small group of cells of the outermost layer of the corpus. Usually three cells in the vertical plane and about three in the transverse plane are involved. The hypodermal cells adjacent to this group become densely cytoplasmic and radially elongated (Fig. 8). The division of the sub-hypodermal cells and the elongation of the hypodermal cells are together responsible for the appearance of the first slight bulge on the axis representing the young primordium.



Figs. 8–12.—Sections of *Cyperus eragrostis*. *d*, dermatogen; *h*, hypodermis; *gl*, glume; *fp*, flower primordium; *c*, carpel; *i*, integument; *mmc*, megaspore mother cell; *gp*, growing point of flower primordium. Longitudinal sections of apex spikelet (Fig. 8); of flower primordia (Figs. 9–10); of ovule (Figs. 11–12.) In Figures 9–12 the axis of the spikelet is on the left.

Although divisions in the hypodermis on the periphery of the young flower primordium may be inclined, periclinal divisions rarely occur in cells of this layer. (In Fig. 8 a periclinal division in the hypodermis is shown and the cells of the hypodermis are rather more elongated than usual.) Cells of the dermatogen never divide by periclinal walls during the formation of a flower primordium. The cells of the dermatogen are therefore derived exclusively from the dermatogen of the axis. Similarly cells of the hypodermis are derived solely from the hypodermis of the axis. Usually, though not always, the corpus of the flower primordium is derived only from the corpus of the spikelet axis.

The early stages of stamen initiation could not easily be established because only one-third of the flowers were hermaphrodite and the stamen could be situated either on the anterior or the posterior side of the primordium. Observations are limited to the development of the unisexual female flower.

The carpels arise by the periclinal division of dermatogen cells in a ring around the apex of the flower primordium (Fig. 9). Periclinal divisions in hypodermal cells in the same area take place subsequently (Fig. 10). These divisions thus occur in the reverse order to that which is found in *Scirpus* and in the Gramineae (Barnard 1957). However, derivatives of the dermatogen cells again constitute the bulk, if not all, of the tissue of the carpels. As the carpels develop, the cells of the apex of the flower primordium become more densely cytoplasmic and the apex elongates rapidly. The integuments differentiate by the division of dermatogen cells. The spore mother cell is formed as the ovule commences to bend away from the axis (Fig. 11). A cell of the hypodermis divides by a periclinal wall to give rise to a parietal cell and the megaspore mother cell. The parietal cell divides then by anticlinal walls (Fig. 12). The ovule and megaspore mother cell enlarge considerably before the megaspore mother cell divides to a linear tetrad. At this stage the ovule is anatropous. From the base of the funiculus on its abaxial side a small group of elongated and presumably secretory cells arise. These cells project to, and almost into, the micropyle. In some young female flower primordia periclinal divisions in hypodermal cells (Fig. 9) and dermatogen cells (Fig. 10) were observed, which were not associated with the formation of a flower part. It is probable that these divisions are a vestigial expression of a perianth.

V. Carex appressa

(*a*) *Morphology*

In *Carex appressa* R. Br. the inflorescence is a long narrow spike-like panicle with inconspicuous bracts. The spikelets are about 5 mm long with spirally arranged imbricating glumes. On each spikelet some 17–25 flower primordia are formed but a number of the distal ones fail to reach maturity. The basal three to six glumes subtend female flowers, while the upper ones subtend male flowers.

In neither male nor female flower is a perianth developed. The male flower consists only of three stamens (Plate 1, Fig. 6). The gynaeceum of the female flower is enclosed in a flask- or bottle-shaped structure (the utricle or perigynium). The styles project through the opening of this structure which is persistant and envelops the fruit (Plate 1, Fig. 6).

The morphological interpretation of the female "flower" and the perigynium of *Carex* and related genera in the Caricae has been the subject of much discussion. Snell (1936), on anatomical evidence, has substantiated the opinion that the pistillate "flower" of *Carex* is in fact a spikelet bearing a single naked pistillate flower. The axis of the spikelet is aborted above the point of attachment of the pistil. The perigynium was believed by Payer (1857) to be composed of two fused bracts. Plate 1, Figure 4, shows that its strongly bicarinate form is well developed at a very early age and it appears to consist of two opposing structures. According to Snell (1936) and Holttum (1948) however, the perigynium represents a single bract of a prophyll nature and is indeed the sheath of the first foliar structure on the spikelet axis. In Plate 1, Figure 7, the single nature of perigynium is apparent during its origin. It would, indeed, seem to be a foliar structure which originates on the posterior side of the axis of the female "spikelet" and encircles it. This point is discussed further under (*b*) below.

(*b*) *Histogenesis*

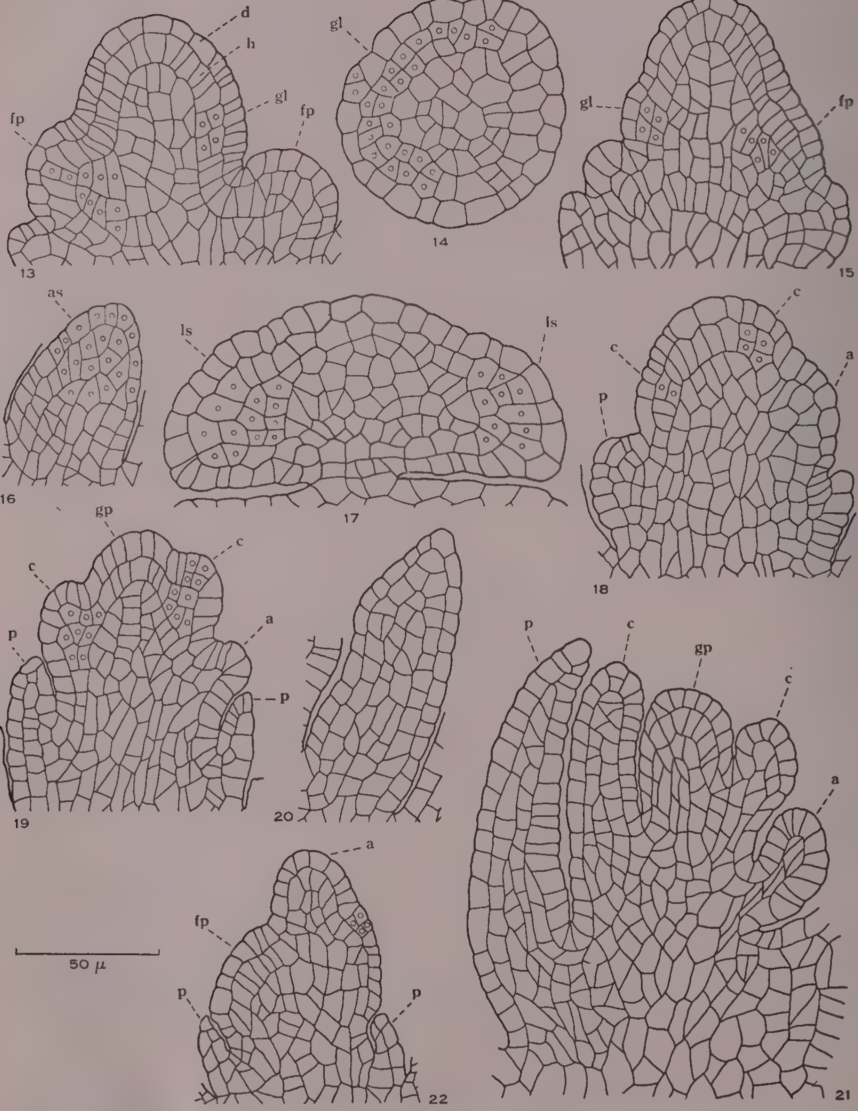
The cells of the apex of the spikelet of *Carex*, as in *Scirpus* and *Cyperus*, are organized into a dermatogen, hypodermis, and corpus (Figs. 13 and 15). The glumes and flower primordia arise from the apex in a spiral sequence with an angular divergence of emergence of about 135°. There is some variation in the angular divergence both within and between spikelets but not so much as in *Scirpus*. The branches of the inflorescence arise in a spiral sequence with a comparable angular divergence, but, as they develop, they became orientated in three vertical rows (Plate 1, Fig. 5).

The glumes are initiated by periclinal division of hypodermal cells (Figs. 13, 14, and 15) and the further division of these cells results in the formation of a crescentic ridge around almost half the circumference (Fig. 14) of the axis. Periclinal divisions of dermatogen cells are rare until the primordium has developed to this stage; they then occur along the crest of the ridge as in the species described above. There seem to be developed, indeed, a number of apical cells along the crest of the ridge. These cells divide repeatedly and give rise to a large part of the tissue of the young glume.

The first signs of the differentiation of a male flower primordium are evident in an enlargement and increase in density of staining of hypodermal cells just above the young glume. The division of these cells continues to be by anticlinal walls but the walls are slightly inclined around the periphery of the region of initiation, and tend to be orientated at right angles to the centre of the initiation. This results in the formation of a slight bulge upon the axis. A small group of cells of the sub-hypodermal layer below the centre of this bulge (Figs. 13 and 15) divide by periclinal and inclined walls. No periclinal divisions occur in the dermatogen. Occasionally, near the centre of the young primordium and on its lower periphery, hypodermal cells may divide by periclinal walls. Thus, as in *Cyperus*, the dermatogen and hypodermis of the flower primordium are derived from the dermatogen and hypodermis respectively of the apex of the spikelet axis. The corpus, though predominantly derived from the corpus of the axis, also includes derivatives of the hypodermis of the axis.

The three stamens differentiate from the flower primordium at a very early stage. Their formation involves practically the whole flower primordium. Neither in radial nor tangential longitudinal section could a residual apex be discerned with certainty. It is certain that cells of the dermatogen never divide by periclinal walls during stamen formation. Their origin is in the merismatic activity of sub-dermatogen cells.

The female "flower" primordium, before the differentiation of any parts, is a conical structure with the cells arranged in a two-layered tunica and central core. Subsequent development shows clearly that it is, indeed, a reduced spikelet axis. The perigynium arises by the periclinal division of dermatogen and hypodermal cells (Figs. 18 and 19). Initiation commences on the anterior side of the axis but subsequently extends completely around the axis. Derivatives of dermatogen cells give rise to most of the tissue of this structure. A female flower primordium arises on the anterior side of the spikelet axis in the same manner as described above for the male flower primordium (Figs. 18 and 19). The flower primordium develops rapidly whilst the apex of the spikelet aborts (Figs. 18, 19, and 21). Abortion com-



Figs. 13–22.—Sections of *Carex appressa*. *d*, dermatogen; *h*, hypodermis; *gl*, glume; *fp*, flower primordium; *as*, anterior stamen; *ls*, lateral stamen; *gp*, growing point of flower primordium; *p*, perigynium; *c*, carpel; *a*, aborted apex of female spikelet.

Figs. 13–15.—Longitudinal section of apex of spikelet. Fig. 14.—Transverse section of apex of spikelet. Figs. 16 and 20.—Radial longitudinal section of male flower primordium. Fig. 17.—Tangential longitudinal section of male flower primordium. Figs. 18–21.—Longitudinal section of female "flowers". Fig. 22.—Longitudinal section of female "flower" with spikelet axis unusually well developed. In Figs. 16 and 18–22 the axis of the spikelet is on the left.

mences with the loss of cell content and because of this the aborting area is very clearly defined in section (Plate 1, Figs. 8 and 9). Occasionally, abortion of the apex is delayed and the lateral origin of the flower primordium in these cases is more clearly observed. In Figure 22 a young primordium in which the spikelet axis has developed further than usual is illustrated. Periclinal divisions in the dermatogen on its anterior side indicate the commencement of the second bract upon it. Examples were observed in which the development of the spikelet axis developed further than illustrated in Figure 22. These "abnormalities" occurred most frequently in the first-formed or lowest primordia.

The initiation of the carpels is by the periclinal division of hypodermal cells in a ring around the apex of the flower primordium followed by similar divisions in the dermatogen. Growth of the carpels proceeds as described in *Scirpus*. Development of the ovule was not studied.

VI. Discussion

The organization of the tissues of the apex of the spikelet is similar in the three species studied and similar to that in the apex of the spikelet of the Gramineae (Barnard 1957). In all species there is a dermatogen, hypodermis, and central core. The organization of the apex of the spikelet is similar to that described by Rösler (1930), Kleim (1937), and Sharman (1945) for the vegetative apex of species of the Gramineae. According to Stant (1952), however, the number of tunica layers in the vegetative apex of *Carex* varied in different species but was constant for one species. Stant also reports that no periclinal divisions in the tunica were associated with leaf initiation. These conclusions appear open to doubt.

The principal differences in the structure of the apices of the spikelets in the Gramineous and the Cyperaceous species are in the size and arrangement of the glumes and flower primordia. The apex is more massive in *Scirpus* than in *Cyperus* in the same way as that of *Bambusa*, for instance, is larger than that of *Lolium*. Cell number and cell size are both responsible for these differences. In *Cyperus*, where the glumes arise alternately on each side of the axis but in one plane, the general appearance of the apex is remarkably similar to that of species of the Gramineae with many flowered spikelets. In *Scirpus* and *Carex*, where the arrangement of glumes upon the axis is in the form of a spiral, the general appearance is somewhat different from this.

In the Gramineae, periclinal division of dermatogen cells invariably follows the first periclinal divisions of hypodermal cells in the origin of the foliar structures such as the lemma. In the Cyperaceae periclinal divisions generally occur in the dermatogen only after several periclinal divisions of hypodermal cells have occurred and the young primordium is already obvious as a crescentic protuberance. In the Gramineae, the hypodermis always contributes to the tissues of the glume or lemma primordia, less frequently to that of the lodicules and palea and only occasionally to the carpel. A similar trend has been observed in the Cyperaceae. The hypodermis contributes largely to the formation of the glume primordia. A greater proportion of the tissues of the perianth members in *Scirpus* and the perigynium in *Carex* are derived from the dermatogen and the bulk if not all of the carpellary tissue is

derived from the dermatogen. The integuments of the ovule arise almost exclusively from the dermatogen. Thus divisions of both the hypodermis and dermatogen are concerned in the origin of these "foliar" organs though the extent of cell division which occurs in their derivatives varies. It varies in the same direction in both families.

The mode of origin of the flower primordia is also essentially the same in the Gramineae and Cyperaceae, and is comparable with the origin of the vegetative axillary bud in the Gramineae as described by Sharman (1945). Periclinal divisions in the dermatogen never occur in the initiation of these structures. The degree of periclinal division in the hypodermis varies in species of the Cyperaceae as it does in the Gramineae. Similarly, in the origin of the stamen, periclinal divisions never occur in the dermatogen. The bulk of the tissue of the stamen primordium is derived from hypodermal cells. An increase in the staining density of hypodermal cells within the area of differentiation is a characteristic feature in both flower primordia and stamen initiation.

The carpels arise as a continuous ring or ridge around the apex of the flower primordium. Later three peaks, one anteriorly placed and two in latero-posterior positions, arise from the crest of this ridge. In the species with a trifid style, each of these peàks develops into one of the stylar branches. In those species with a bifid style, it is the anteriorly placed peak which fails to develop. Failure of the anterior carpel to develop is also a feature of the Gramineae. In the Gramineae, the anterior carpellary tissue is initiated before that on the posterior side of the flower primordium and, in its initial stages, develops more rapidly. The posterior carpellary tissue arises higher on the flower primordium axis than that on the anterior side.

The apex of the flower primordium in the Cyperaceae is transformed directly into the ovule as it is in the Gramineae. Likewise the ovule turns away from the spikelet axis and bends into an anatropous position. The only real difference between the two families is that in the Gramineae the ovule appears to be placed excentrically in the ovary while in the Cyperaceae it is centrally placed. The adaxial placement of the ovule in the Gramineae would seem to be associated with the earlier and more rapid development of the anterior carpellary tissue relative to that on the posterior side of the axis. The argument of Blasser (1941*b*) that the excentric position of the ovule in the Gramineae indicates derivation from a previous parietal placentation does not seem to be well founded. Further, the argument of Blasser that the vascular structure of the gynaeceum and floral axis of the Cyperaceae provide evidence for the derivation of the ovule in this family from a previous free central placentation is somewhat speculative. An examination of the vascular structure of the gynaeceum in *Scirpus validus* shows it to be much more complicated than that which occurs in the Gramineae. It would seem that any conclusions derived from the observable structure would have to be highly speculative, requiring considerable imagination. Derivation of the ovule from either a terminal position or a lateral position axillary to an anteriorly placed carpel seems more acceptable.

In the Gramineae, floral structure is on the whole remarkably uniform. Variation in inflorescence and spikelet form associated with a reduction in the number of florets per spikelet seems to have been the principal feature of evolutionary develop-

ment. In the Cyperaceae, on the other hand, floral structure shows considerably more variation. Thus in *Scirpus* the flower is of the "typical" monocotyledonous form; in *Cyperus* the perianth members are absent, unisexual flowers occur and members of the androecium have been lost; in *Carex* perianth members are absent, the terminal spikelet on an inflorescence branch consists of male flowers and the lateral spikelets have been reduced to a single female flower. The perigynium is undoubtedly a foliar structure which occupies the prophyll position on the axis of the reduced spikelet. It would seem therefore that in this family floral structure has evolved along a number of distinct and separate pathways. The pattern of histogenesis of individual floral organs has remained remarkably constant.

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Explanation of Plate 1

Photomicrographs of *Scirpus validus* and *Carex appressa*.

Fig. 1.—The distal portion of a young spikelet of *Scirpus* showing the spiral arrangement of glumes and flower primordia. In the most advanced flower primordium two members of the outer (*op*) and two of the inner perianth whorl (*ip*) are visible. The three stamens (*s*) and three peaks on the carpellary ridge are also shown. ×85 approx.

Fig. 2.—A flower primoridum of *Scirpus* viewed from the posterior side. *s*, stamen; *op*, outer perianth; *ip*, inner perianth. ×95 approx.

Fig. 3.—Posterior view of young flower of *Scirpus*. ×80 approx.

Fig. 4.—Young female "flower" of *Carex* attached to the axis. The bicarinate perigynium (*p*) encloses the gynaeceum which has two carpellary peaks (*c*). ×80 approx.

Fig. 5.—Young inflorescence of *Carex*; the primary branches arise in spiral sequence and subsequently become disposed in three vertical rows. × 25 approx.

Fig. 6.—A young male flower (left) and a young female flower (right) of *Carex*. ×30 approx.

Fig. 7.—Transverse section of young female "flower" primordium of *Carex* showing posterior origin of perigynium. The axis of the spikelet is on the left side. ×320 approx.

Fig. 8.—Longitudinal section of female "flower" primordium of *Carex* showing aborting apex of spikelet (area with light stained cells). ×370 approx.

Fig. 9.—Longitudinal section of female "flower" of *Carex* showing aborted spikelet apex (*a*) and carpellary tissue (*c*) arising. The perigynium is at (*p*). ×330 approx.

FLORAL HISTOGENESIS IN THE MONOCOTYLEDONS. II

THE REGENERATION OF SEVERED PEA APICES

By Heather F. Gulline* and Rona Walker*

[*Manuscript received October 4, 1956*]

Summary

Successful graft unions between meristematic tissues have been made in apices of the pea, *Pisum sativum* L. A technique for preventing desiccation of apices during and after the operations was developed. Apical segments ranging from about 200μ down to 50μ in depth were successfully grafted back to their parent plant. The subsequent development of grafted apices was completely normal. These experiments show that a complete shoot can be regenerated from an apical segment less than one-thousandth of a cubic millimetre in volume, containing about 600 cells. This is smaller than any graft previously recorded.

I. Introduction

The experiments described here were initiated by a study (McAulay, unpublished data) of the morphogenetic action of small pea buds grafted into differentiated tissue. McAulay found that bud initials of a volume of less than one-hundredth of a cubic millimetre could not be grafted successfully into mature stems. The question then arose whether this failure was due to some "ungraftability" of apical tissues, or to other causes. Experiments were commenced on the removal and replacement of small axillary bud initials upon their own bases. It was considered that, if severed apices were capable of being grafted, this was the most favourable position for successful healing and development.

The only previous attempt to remove and replace meristematic plant tissues is that of Ball (1950). Using *Lupinus albus* L., Ball found that small portions cut out of the apical meristem could not be grafted back to their original positions. Such isolated apical sectors usually died, apparently following desiccation. Those which remained alive never resumed their normal function of controlling the growth of the shoot. From further experiments with vertically bisected apices of *Lupinus*, Ball (1955) concluded that "apical tissues are seldom, if ever, graftable".

In the course of experiments in this laboratory a technique for preventing desiccation of small grafts during and after the operations was developed. Use of this technique, which will be described in detail in the next section, has shown that, contrary to Ball (1950, 1955), it is possible to graft small segments of apical tissue. Slices cut from the tops of apices as small as $150\,\mu$ wide and $50\,\mu$ high and containing about 600 cells have been successfully reunited with the parent apex, developing into normal buds.

Experiments of this type are important in establishing the position of the organizing centre of the apex. The theory that the entire growth of a shoot develops from the top few layers of apical cells is experimentally confirmed.

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II. Materials and Methods

Young seedlings of the green pea, *Pisum sativum* L. var. "Onward", were used. The seeds were sterilized by soaking for 5 min in 1 per cent. bromine water to kill seed-borne organisms, washed thoroughly with distilled water, and soaked overnight in tap water. The testas were removed and the seeds placed on moist filter paper to germinate. When the radicle was about $1\frac{1}{2}$ in. long, each seedling was placed in a segment of glass tubing kept within a 4 by $1\frac{1}{8}$ in. glass tube with a cotton wool stopper. Dry cotton wool was packed round the radicle immediately below the cotyledons to hold the seedling firmly in the tubing. The tip of the radicle dipped into water or wet cotton wool. A 3 by 1 in. microscope slide kept the inner glass tube in an upright position inside the outer tube (Fig. 1).

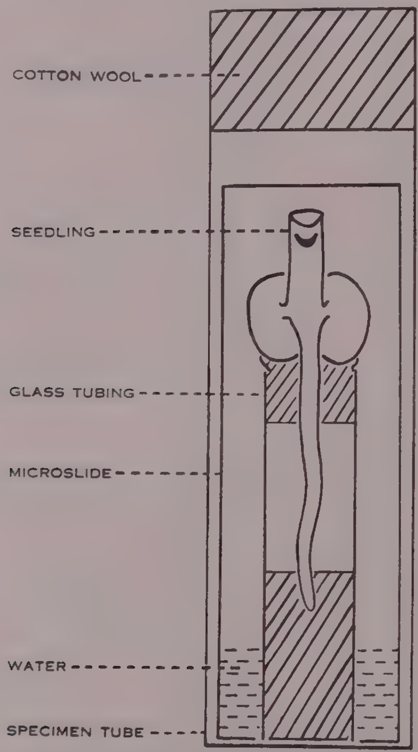

Fig. 1.—Method of growing seedlings during experiments. Seedling shown with leaf removed, decapitated above first node. Actual size.

The atmosphere within the tube was moist but not saturated. No nutrient substances were supplied to the plants.

The seedlings were decapitated above the first node at approximately a week after germination. The bracts and all axillary buds developed beyond the stage of an apex with one leaf primordium were removed. After this pruning, a succession of apices arose in each axil (see Plate 1, Fig. 1). At least 2 days were allowed for

recovery from shock and the initiation of active growth of the axillary apices before experiments commenced. These new apices were especially convenient because no further damage to the plant was necessary for subsequent observation. If leaf initials were left below a grafted apex, they could obscure it in one day's growth. It would then be necessary to remove them, with inevitable shock and damage, to allow the developing apex to be seen.

Knives made from pieces of thin razor blade clamped on to brass holders were used for the operations. These were sterilized in absolute alcohol before each operation.

During the operations, the plants were kept in a glass-topped box in whose atmosphere an atomizing spray maintained a fine mist of water droplets. Conventional methods designed to keep the atmosphere around the apex saturated were insufficient and the apex dried up when viewed in a strong light. The atmosphere of fine water droplets overcame this desiccation and was vital to the success of the experiments. A Baker high-power dissecting microscope was mounted above the glass top with one strong lamp on each side. The operator's hands entered the box through a space at the front, curtained with plastic sheeting to retain the saturated atmosphere. The axillary apices of "Onward" peas used in these experiments are 120–180 μ wide by 50–80 μ high.

Measurements of the apices were made by means of an ocular micrometer. The number of cells constituting an apex was estimated as follows: measured apices typical of those used in the experiment were individually macerated in drops of acid aceto-orcein stain fixative on microscope slides. A cover-slip was placed over the apex and tapped gently until the cells separated. An accurate count of the cells could then be made under a microscope. Toward the end of a plastochron an apex comprises about 900 cells. An apex with one leaf primordium visible as a ridge is usually about 200 μ wide and contains 1500–2000 cells.

For histological examination, grafted buds were removed from the plants with a few millimetres of subjacent tissue, fixed in formalin-acetic-alcohol or 3 : 1 alcohol-acetic fixative, dehydrated, paraffin-embedded and sectioned at 10 μ. Sections were stained with Ehrlich's haematoxylin, Heidenhain's haematoxylin and light green or Bismarck Brown Y, or crystal violet.

III. Experimental Procedure

In preliminary experiments, developing buds with one or two leaf primordia were cut incompletely through, remaining attached by a fragment of epidermal tissue at one point. When it was found that buds so cut would reunite with their bases, further experiments were carried out with completely severed and reoriented apices. Shoot tips were severed by a transverse cut at a level of 200 μ or less below the summit of the apex itself. Bud initials with visible leaf primordia were rotated through approximately 180° after cutting, to ensure that the existing conducting paths of growth substances and food materials were interrupted. This was done to provide an approximation to the conditions in grafts from one plant to another. Smaller bud initials, of 150 μ or less in height, tended to stick to the knife so that their orientation on replacement was a matter of chance. Apices were touched as

little as possible as any damage or pressure usually led to their death. Successively shallower pieces of apical meristem were severed and replaced, the smallest being only 20 μ deep. Plate 1, Figure 1, shows a longitudinal section through two young axillary buds at the first node of a *Pisum* seedling. The smaller, *a*, is typical of the apices used in these experiments; the larger, *b*, illustrates the normal development of an uncut apex.

No mechanical aids were used to hold an apex in contact with its cut base. The liberated contents of cells destroyed in cutting acted as an adhesive. It was found that washing cut apices to remove damaged material always resulted in their death.

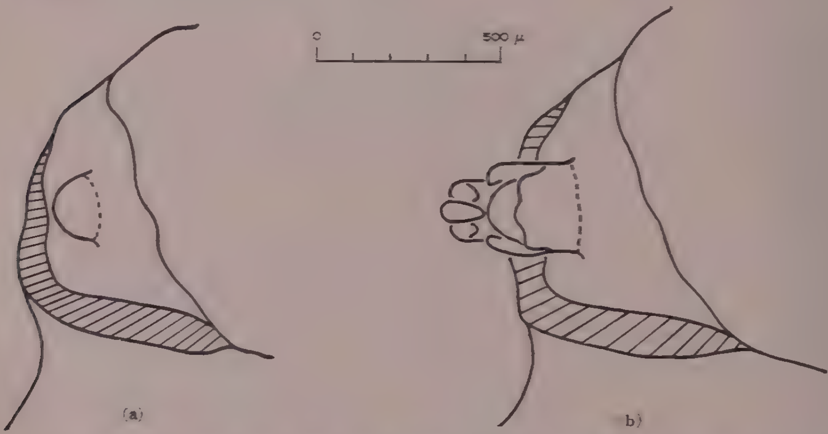

Fig. 2.—A grafted apex (*a*) on day of cutting, (*b*) after 7 days. The position of the cut is shown by the broken line.

Freehand sketches, with measurements, were made of the progress of apices after cutting. Photographs were taken through the dissecting microscope of severed apices which looked promising. A series of drawings reproducing the photographs obtained in one such case has been prepared (Fig. 2).

IV. Results

In the severed apices which grew, three types of development occurred:

(i) Apices which had grown slowly for a few days became dormant and finally died. When these apices were sectioned it was found that there was no cellular continuity whatever between the severed apex and its base. True growth had occurred, with cell division and formation of new leaf primordia, as well as increase in size of the apical portion. Differentiation had also proceeded in the provascular strands. It is evident that nutrient materials had diffused across the wounded cell fragments at the junction of the cut surfaces. Later uneven growth forced the cut surfaces apart, causing grafting to become impossible. Plate 1, Figure 2, illustrates an example of this.

(ii) In some cases the apices remained healthy-looking but dormant for periods of up to a month. Growth then began slowly, the rate increasing rapidly after 2 or 3 days' growth. Sections revealed that in these apices a graft union had developed initially through a few cells only, usually in the outer cortical area. Once a vascular connection was made with the graft, development was still further accelerated. In some cases this vascular trace was completed only after a considerable time, having taken an indirect path through the subjacent tissue. In one such case the path was followed and found to approach within 30 μ of the epidermis. In Plate 2, Figure 1, this vascular trace is seen at its closest to the plant surface. The section illustrated was the third from the surface of a series of 10 μ sections through the bud. Plate 2, Figure 2, is a section through the centre of the same bud.

(iii) A few apices commenced to grow 1 or 2 days after cutting and within a week had developed into small buds with young leaves completely enclosing the apex. Plate 1, Figure 3, shows a grafted apex growing vigorously after 4 days. Sections through such buds showed perfect graft unions. Most of the coagulated remains of cells destroyed in the grafting operations were absorbed within a few days, and provascular tissue was continuous between stock and scion. Plate 2, Figures 3 and 4, show transverse sections through the graft areas of perfectly healed buds.

None of the apical pieces less than 50 μ in height was successfully grafted back to the stem tip. The minimum size of an apex which regenerated a bud was 150 μ wide by 50 μ high, comprising 500 to 600 cells. The volume of such a piece was estimated to be about one-thousandth of a cubic millimetre.

Smaller pieces of apex were almost immediately dislodged by the growth of the underlying tissues. In most cases of failure of larger grafts, sections showed that uneven extension or shrinkage of cells of the cut surface forced the stock and scion apart, making cellular connection almost impossible within a very short time. It appeared frequently that the epidermal layer of both the cut apex and its base had expanded. While epidermal cells continued to have some contact, the central cells of both surfaces were isolated from one another. The successful grafts of type (ii) (see above) probably arose from irregular areas of contact. Vascular traces were formed in tissue that would normally be cortical (see Reeve 1948). At this stage in the development of a shoot the destiny of these cells was not unalterable.

No instances of the gaping of cut apices as recorded in other plants by Snow and Snow (1947) and others were observed. There is no evidence of any tension of the epidermal layer in *Pisum*. The instances of expansion of epidermal layers of severed apices recorded in (ii) above indicate the reverse.

Bacterial infection was rarely the cause of failure of grafts. About 20 per cent. of apices which had not commenced to grow within 2 or 3 weeks after cutting eventually became infected through frequent handling. Most of these would probably have failed in any case. Precautions taken during the experiments appeared sufficient to avoid serious losses of successful grafts.

V. Discussion

The experiments reported here have resulted in the first successful grafts of meristematic tissues. As recently as 1955, Ball concluded that apical tissues were ungraftable. The experiments reported here have shown conclusively that meristematic tissues can be grafted successfully. In addition, as far as can be ascertained, the present grafts are smaller than any meristematic tissues grown *in vitro* into normal plantlets.

Very few observations on the healing together of portions of incised apical tissues have been recorded. In the course of investigations into phyllotaxis and the determination of leaves and buds, several workers have made incisions into stem apices (see Wardlaw 1952). Of these, only Snow and Snow (1947) describe the healing together of such cut surfaces with the subsequent development of vascular traces through the healed area.

The first attempts to grow detached plant apices were those of White (1933) who pioneered the *in vitro* culture of plant material. The smallest pieces of apical meristem grown successfully *in vitro* to whole plantlets (Wetmore and Morel 1949; Wetmore 1954) are " from 250 down to 100 μ long and bearing two leaf primordia or even one primordium" (cited in Wetmore and Wardlaw 1951).

Successful grafting of the shoot tips of plants has been reported by only a few authors. Camus (1949) grafted buds 1 cm long into callus tissue *in vitro*, causing differentiation of vascular strands in the callus, beneath and continuous with those of the bud. Wetmore (1953) grafted *Syringa* apices about 250 μ long into callus tissue of the same plant *in vitro* but did not obtain vascular continuity between stock and scion. This appears to be the smallest viable graft recorded previously. However, as pointed out by Ball (1955), it is not strictly comparable with grafts of meristematic tissue to meristematic tissue.

The apical segments of *Lupinus* which Ball (1950) was unable to graft were wedge-shaped, about 100 μ deep and 150–200 μ wide. The volume of these segments was probably about one-thousandth of a cubic millimetre. In the present experiments volumes as small as this were successfully grafted using *Pisum*.

Comparison of photographs of sections through *Pisum* apices (see Plate 1) with those of *Lupinus* apices (Ball 1950) shows that the average size of apical cells is smaller in *Pisum*. Hence the numerical cell content of the grafted *Pisum* apices was greater than that of the isolated segments of *Lupinus* apices. It is possible that the presence of the additional cells surrounding the central initials of the severed apical pieces of *Pisum* enabled them to continue their normal role.

In addition, it seems likely that *Pisum* is physiologically more resistant to wounding and therefore easily grafted. Paton and Barber (1955) recorded better than 90 per cent. successes with grafts in the first internode of young pea seedlings. Grafted apices of *Pisum* never developed such a well-defined wound cambium as that described by Ball in *Lupinus*. In *Pisum*, cell divisions in the layers of cells immediately below wound surfaces appeared to contribute mainly to the normal growth of the plant shoot.

A further factor contributing to the success of the present experiments was the development of the technique by which plants were kept in a mist-laden atmosphere throughout the operations. Until this was introduced, few apices could withstand the dehydration suffered through exposure to strong lamps.

Apical graft unions in the present experiments generally took place by a simple "growing together" of cells in contact across the cut, followed by the development of a vascular trace basipetally through the healed area. After vascular connection with the main stele was effected, rapid growth of the buds and absorption of coagulated dead tissues resulted in the development of healthy normal shoots. When attempted grafts were unsuccessful, the cause was usually found to be spatial separation of the cut surfaces rather than the extensive proliferation of layers of callus cells.

The smallest apical piece successfully grown contained not more than 600 cells. Previous workers have shown that all the cells which later differentiate into the tissues of a plant shoot arise from the divisions of a comparatively few cells of the shoot apex (Dermen 1945; Reeve 1948; Ball 1948, 1954). Although this number is not known for *Pisum*, the smallest of these grafts undoubtedly contained many more cells.

It is felt that the present experiments do not represent the true limit of the amount of apical meristem which can be successfully grafted to resume its normal development. Further reduction in the size of the grafted portion does not appear impossible on morphogenetic grounds. However, the technical difficulties in working with such small portions of apical meristem are great. The chief difficulty appears to be to avoid damage to the apex during the operations. Even touching the surface of an apex, without causing any visible damage, may result in its death. Further progress in this work requires a technique for removing small numbers of cells from an apex without damage to intact cells, and a method of holding stock and scion in close contact without inhibiting the growth of either.

VI. Acknowledgments

The authors wish to thank Professor A. L. McAulay, who first suggested this problem, for his continued interest and criticism. Dr. B. I. H. Scott gave valuable assistance in preparing the final draft of this paper. The work was generously supported by C.S.I.R.O.

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Explanation of Plates 1 and 2

All sections are reproduced at a magnification of × 200.

Plate 1

Fig. 1.—Longitudinal section through the node of a pea seedling, showing axillary buds in normal growth. *a*, apex typical of those used in the experiments; *b*, normal axillary bud developing from an uncut apex.

Fig. 2.—Longitudinal section through an unsuccessful graft. The cut surfaces have been forced apart by expansion of the upper layer of cells.

Fig. 3.—A grafted apex, *in situ*, which has developed two leaf primordia, 4 days after cutting.

Plate 2

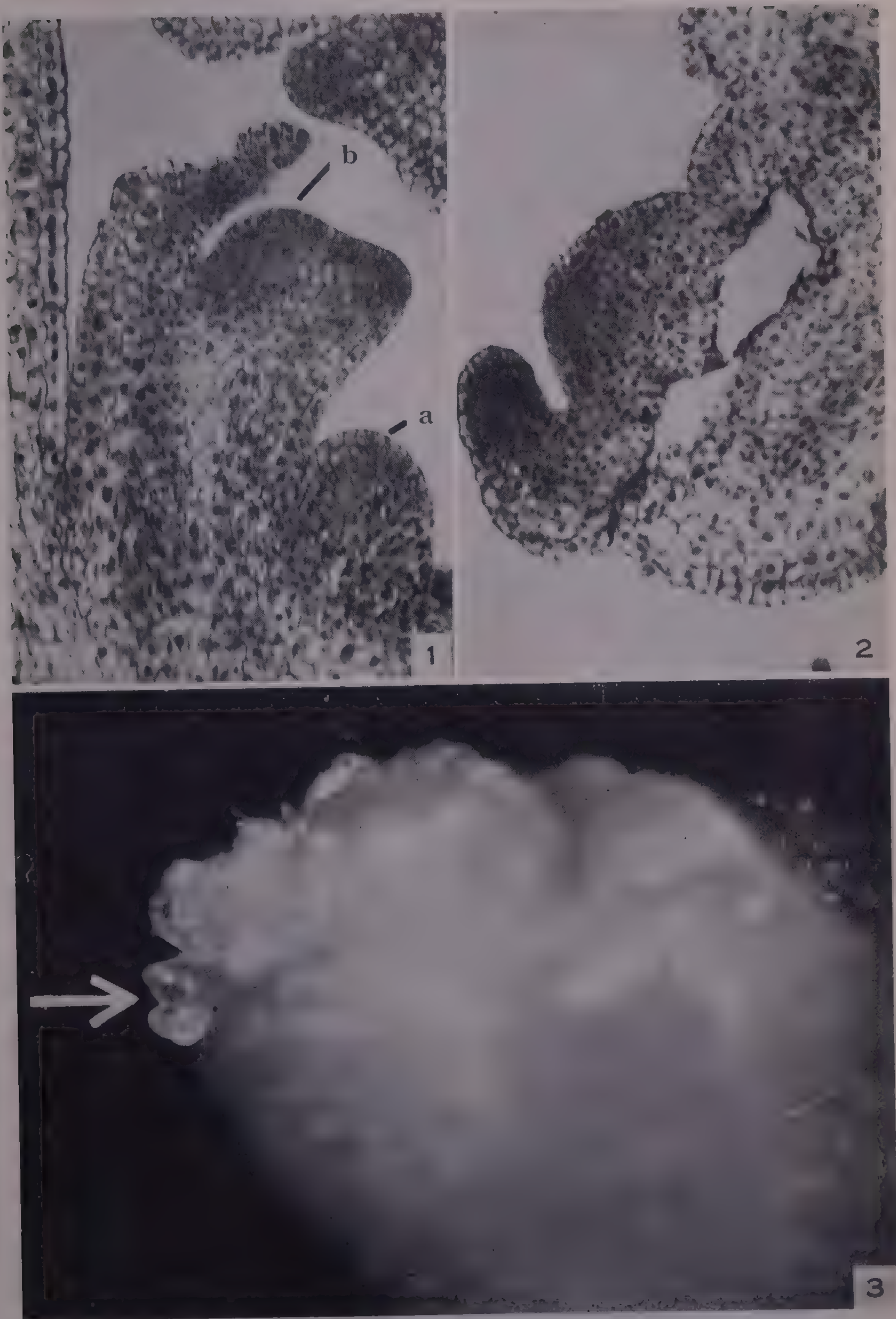
Fig. 1.—Longitudinal section through the healed area of a successful graft. A vascular connection has developed only 30μ below the epidermis.

Fig. 2.—Median longitudinal section through the same bud as Figure 1. In this plane the cut is unhealed.

Fig. 3.—Transverse section through the healed area of a perfectly grafted apex. The only remaining trace of the wound is shown by the arrow.

Fig. 4.—Transverse section through the base of the graft whose progress was shown in Figure 2 in text (p. 132).

THE REGENERATION OF SEVERED PEA APICES



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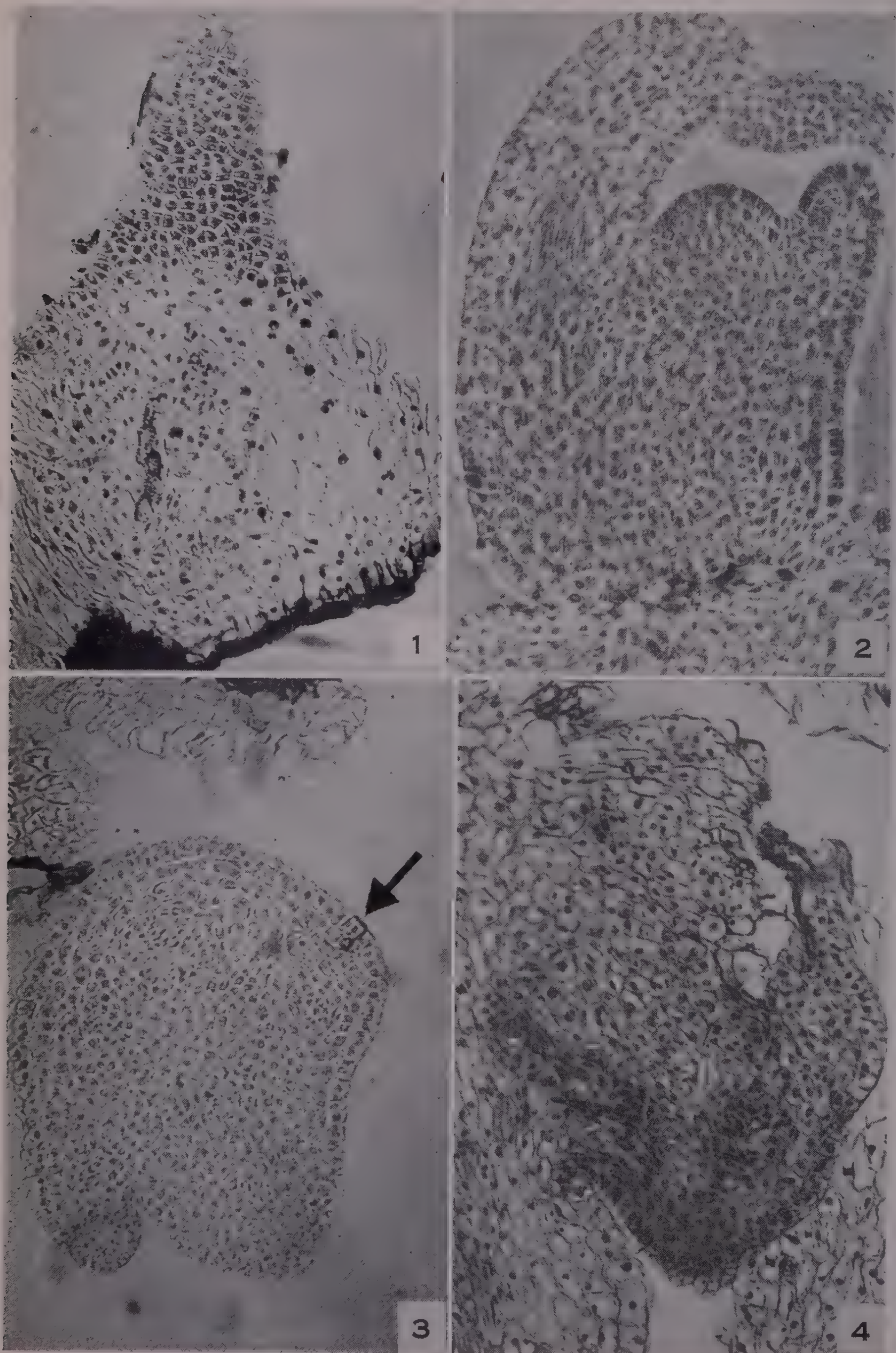

DARK ISLAND HEATH (NINETY-MILE PLAIN, SOUTH AUSTRALIA)

IV. SOIL MOISTURE PATTERNS PRODUCED BY RAINFALL INTERCEPTION AND STEM-FLOW

By R. L. Specht*

[*Manuscript received April* 23, 1957]

Summary

Rainfall interception and stem-flow in the heath vegetation on the Makin sand of the Ninety-Mile Plain of South Australia are discussed. The nanophyllous shrubs, *Banksia ornata* and *Xanthorrhoea australis*, intercept and redistribute a large percentage of the rainfall. Striking differences in soil moisture contents are produced over very small distances; these differences are not conspicuous underneath the leptophyllous undershrubs, although rainfall interception by their foliage and litter may reduce the quantity of water reaching the soil.

I. Introduction

The ability of vegetation to intercept rainfall has excited the interest of many scientists during the last 50 years. Many investigations have been made on forest communities (Horton 1919; Phillips 1926, 1928; Mitchell 1930; Holch 1931; Beall 1934; Lunt 1934; Wood 1937; Kittredge, Loughead, and Mazurak 1941; Wicht 1941; Niederhof and Wilm 1943; Grah and Wilson 1944; Hayes and Kittredge 1949).

Phillips (1926, 1928) has shown that trees may induce the precipitation of fog or mist as droplets on their foliage. This moisture dropped to the ground and was recorded in rain gauges under the trees at a time when no moisture collected in control gauges in the open. It is doubtful whether this induced precipitation, which totalled only 0·015 in. per misty day, is of much physiological value.

Under most rainfall conditions, the canopies of the forest prevent a considerable proportion of the rainfall from reaching the ground. From 15 to 30 per cent. of the rainfall may be intercepted by the foliage. The value varies (i) with the species composition of the forest, (ii) the density of the trees, (iii) the projection of some specimens above the general level of the forest, and (iv) the wind velocity. Kittredge, Loughead, and Mazurak (1941) noted that the average interception percentage was highest on the leeward side of a tree and that this difference in interception increased with the velocity of the wind. This phenomenon is probably the result of the turbulence which exists on the leeward side of any object. Lunt (1934) noted that isolated forest trees intercepted more rainfall near their centres than towards their extremities. The greater density of foliage near the centre of the tree may explain this observation.

Grah and Wilson (1944) examined the components of rainfall interception in the laboratory. They defined three forms of interception: (i) "transitory storage", the water that will drain from a plant under still air conditions; (ii) "conditional storage", the additional water that can be removed by wind or by forceful shaking; and (iii) "residual storage" or the water that can be removed only by evaporation.

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The transitory storage component either falls directly to the ground from the foliage or runs along the leaves and branches. There it may adhere as residual storage, or finally flow down the trunk or from the ends of branches to the ground. The amount of conditional storage which is retained depends upon the wind velocity. Under calm conditions, *Baccharis pilularis* and *Pinus radiata* retained up to 70 per cent. of the rainfall intercepted but, under the influence of strong winds, only 35 per cent. was retained. This retained water either shook off or ran along the leaves and stems to the ground.

The water which runs down the leaves and stems is usually referred to as "stem-flow". Kittredge, Loughead, and Mazurak (1941) found that, of the 17–28 per cent. of the rainfall intercepted by the canopy of a pine plantation, on the average only 1 per cent. reached the ground by stem-flow, but during fierce storms stem-flow was as much as 13 per cent. of the actual rainfall.

The direction of the stem-flow is not always towards the trunk of the tree. McMunn (1936) recorded that apple trees shed a considerable amount of rain near the periphery of the tree ("foliar drip"). A similar observation was recorded by Lunt (1934) in white pine trees.

These phenomena have been observed in grasslands and crops by Horton (1919), Clark (1937, 1940), Haynes (1937, 1940), Kittredge (1938), and Reimann, Van Doren, and Stauffer (1946). Rainfall interception by these communities may be even higher than that of the forests. Values as high as 75 per cent. of the total rainfall have been reported, but the values vary with the intensity of rainfall, the density of the foliage, and the environmental conditions. Only a few species, such as corn, lucerne, and soybeans, showed stem-flow.

Similar results have been reported from the chaparral of California, a community similar in structure to the heath vegetation of southern Australia. Bauer (1936) showed that about 35 per cent. of the rainfall was intercepted. Some of this reached the soil by stem-flow; the rest was returned to the air by evaporation. Species with smaller leaves intercepted less rain than those with larger leaves.

Hamilton and Rowe (1949) observed the "through-fall", "stem-flow", and "interception storage" in three localities in chaparral. Of the total rainfall 62–81 per cent. reached the soil directly; 8–30 per cent. flowed down the stems; while 5–11 per cent. was held on the foliage and lost to the air by evaporation.

Interception of rainfall by vegetation is a major factor in any investigation of the water balance of an ecosystem. Stem-flow or foliar drip, which can be of considerable importance in certain plant communities, enables some of this intercepted water to reach the ground; the rest is evaporated. The resultant soil moisture patterns which may be produced by such phenomena as stem-flow or foliar drip have received little attention.

During an examination of the root systems of the heath vegetation on the deep Makin sand in the Ninety-Mile Plain of South Australia (Specht and Rayson 1957*b*), considerable differences were observed in the soil moisture under two of the species, *Banksia ornata** and *Xanthorrhoea australis*. Detailed observations over

* Nomenclature follows that used in Part I of this series (Specht and Rayson 1957*a*, Appendix I).

a period of 2 years established the presence of striking soil moisture patterns under these species. The results of these observations are presented in the present paper.

II. Methods

At monthly intervals, a site was chosen where one specimen of each of the species, *Banksia ornata*, *Xanthorrhoea australis*, and if possible *Casuarina pusilla*, occurred in a line 6–7 ft long. A pit, 7 ft long and 6 ft deep, was dug to one side of this line. The side of the pit nearest the specimens was then gridded into 1-ft squares with further horizontal subdivisions within the surface foot at depths of 3 and 6 in. The aerial vegetation and the root systems exposed in the face of the pit were accurately sketched. Samples of the sand were collected in duplicate in airtight tins about 3 in. in from the face of the pit at each of the grid intersections. Samples at a greater depth than 6 ft were collected by means of an auger inserted at 1-ft intervals into the clay subsoil. Most fragments of roots were removed from the sample before the tin was sealed. The tins were weighed as soon as possible after sampling, opened, and the contents dried in an oven at 95°C to a constant weight. The soil moisture was expressed as a percentage of the dry sand. Isolines of equal percentage soil moisture were then plotted on the grid under a sketch of the vegetation.

Changes in the soil moisture pattern could not be observed at precisely the same site throughout the period. With the procedure used, slight differences were bound to occur in the spatial relationships of the vegetation, depth of sand, and even microclimate within short distances (Rayson 1957). These may have reflected themselves in differences in the soil moisture pattern. However, it was impossible to install the battery of moisture meters needed to gain a picture of the pattern without severely disturbing vegetation and soil. By the time the vegetation had re-established itself (at least 10 years) most moisture meters would have been installed longer than their useful life-span. Furthermore, no moisture meter has yet been devised which will alone satisfactorily cover the range of soil moistures encountered in this almost pure sand.

In spite of the small variations which may be expected from the changes in the site from month to month, the soil moisture patterns which were obtained were strikingly consistent.

III. Results

(a) *Patterns of Soil Moisture*

A representative set of eight of the 24 diagrams which were constructed at monthly intervals over a period of 2 years is illustrated in this paper.

Figure 1 indicates the status of the soil moisture towards the end of the summer period. Temperatures had been high and rainfall negligible for several months (Specht and Rayson 1957*a*); the soil moisture of the whole profile, irrespective of the above vegetation, had fallen to a level at or near that of the permanent wilting point.* Any small variations which were observed between sampling positions on

* The permanent wilting point was determined by Mr. J. Holmes, of the Division of Soils, C.S.I.R.O., Waite Agricultural Research Institute, Adelaide, by means of the pressure membrane apparatus, at a pressure of 15 atm. The permanent wilting point for the A_1 organic horizon was 1·00 per cent., that of the deep A_2 horizon 0·70 per cent., while the sandy clay to clay subsoil varied from 7·0 to 17·1 per cent.

the diagram were insignificent and were due to variations in the small quantities of organic matter and root material which were included in the samples.

A heavy shower of rain either during the summer or at the break of the season immediately wetted the surface soil, the depth of penetration depending on the amount of rainfall. Specimens of *Banksia ornata* and *Xanthorrhoea australis* intercepted a large percentage of the rain which fell on their foliage and, by the orientation

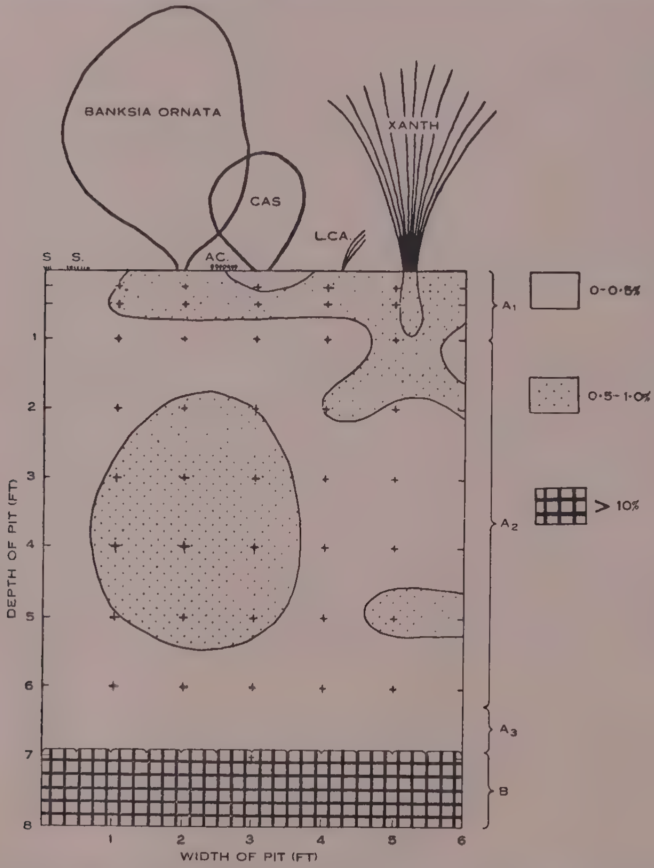

Fig. 1.—Soil moisture pattern under the heath vegetation towards the end of the summer period (Feb. 3, 1951). The crosses indicate the sampling points. The species present were *Banksia ornata*, *Xanthorrhoea australis*, (XANTH.), *Casuarina pusilla* (CAS.), *Acrotriche affinis* (AC.), *Lepidosperma carphoides* (L.CA.), and *Schoenus tepperi* (S.).

of their leaves, directed much of it down their leaves and stems to the ground. Thus a rain-shadow was created under the periphery of the plants with a region of rainfall accumulation towards the centre. The water entered the ground near the trunk of *Banksia ornata* at ground level, but, in *Xanthorrhoea australis*, flowed down between the buried leaf-bases to enter the soil at the stock (caudex) some 9–12 in. below the surface (see Specht and Rayson 1957*b*, Fig. 2). This

irregular microdistribution of the rainfall was well expressed in the resultant soil moisture patterns (Fig. 2) which were recorded 2 days after a fall of 0·96 in. of rain. The A_1 horizon had been moistened by the rain and cones of moisture had penetrated well into the A_2 horizon under the specimens of *Banksia ornata* and *Xanthorrhoea australis*. The soil at the centre of the cones was near field capacity; less than a foot away it was still at wilting point.

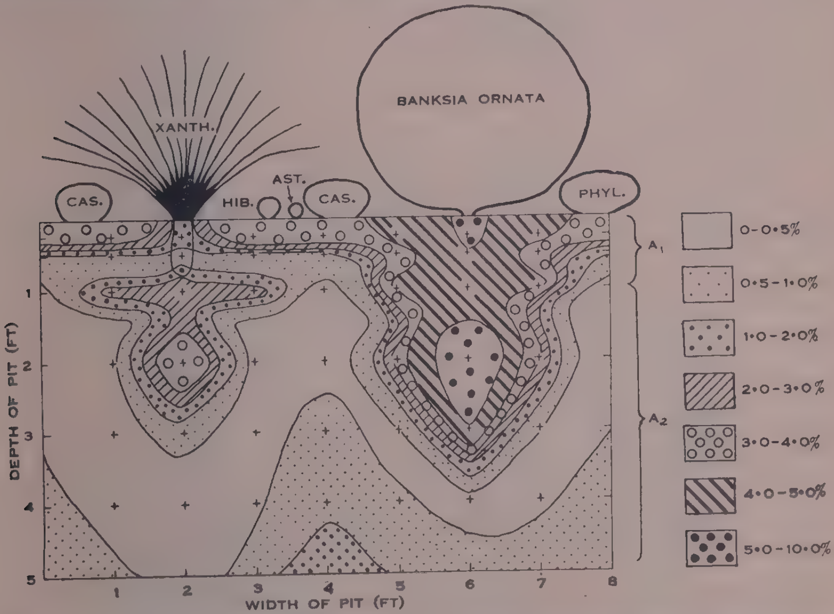

Fig. 2.—Soil moisture pattern under the heath vegetation after 96 points of rain had fallen on to a profile near its wilting point throughout (March 20, 1950). The species present were *Banksia ornata*, *Xanthorrhoea australis* (XANTH.), *Casuarina pusilla* (CAS.), *Hibbertia stricta* (HIB.), *Phyllota pleurandroides* (PHYL.), and *Astroloma conostephioides* (AST.).

It is possible to calculate the rainfall which is stored in the soil by the formula

$$R_s = \frac{D.P. \times W \times Sp.G.}{100}, \quad \ldots\ldots\ldots\ldots\ldots\ldots (1)$$

where R_s is the amount of rain (in inches) stored in the soil, *D.P.* is the depth of penetration in inches; *W* the percentage of moisture and *Sp. G.* the apparent specific gravity of the soil.

The apparent specific gravity of the horizons of the Makin sand was determined to be 1·37 and 1·36 for the A_1 and A_2 horizons respectively. The amount of rainfall stored above the wilting point was calculated for each of the vertical grids of Figure 2. About 0·89 in. of rain were stored vertically under the stock of the *Xanthorrhoea*; 0·23 in. one foot to the right; 0·19 in. at the next vertical grid; 1·38 in. vertically under the edge of the *Banksia*, and 2·54 in. directly underneath the trunk of this specimen. These figures emphasize the rain-shadows which were produced at the edge of these plants and the accumulation of moisture by interception and stem-flow.

It is possible to use the roughly geometrical figures which compose the soil moisture patterns of Figure 2, either as plane or (on the assumption that the pattern is still symmetrical) as three-dimensional figures, to calculate the total amount of rainfall stored under this vegetation. These calculations indicated that 90 per cent. of the 0·96 in. of rain which fell on the site was stored in the soil 2 days later. This indicated that most of the other 10 per cent. was held on the foliage and lost by evaporation. Transpiration during the interval of 2 days also played a small part.

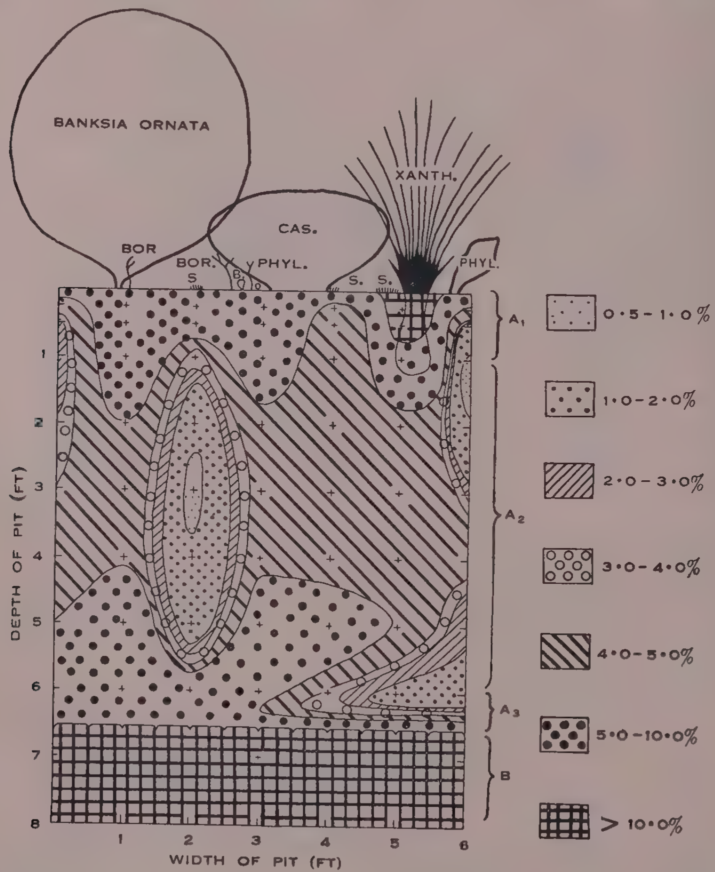

Fig. 3.—Soil moisture pattern under the heath vegetation towards the middle of winter (June 3, 1950). The species present were *Banksia ornata*, *Xanthorrhoea australis* (XANTH.), *Casuarina pusilla* (CAS.), *Phyllota pleurandroides* (PHYL.), *Boronia caerulescens* (BOR.), *Baeckea ericaea* (B.), and *Schoenus tepperi* (S.).

However, an examination of the soil moisture data under each species showed that only 55 per cent. (20 per cent. by rain falling between the leaves and 35 per cent. by leaf-flow) of the rain which fell on the area occupied by the specimen of *Xanthorrhoea australis* reached the soil; 20 per cent. more moisture was held in the soil under *Banksia ornata* than fell as rain on the area covered by the bush. This

excess may be attributed to approximations in the calculations, irregularities in the rainfall, or more probably to a small residuum of soil moisture which was left from a heavy shower of 1·24 in. a month before. Such residua were often noted under the dense shade of the *Banksia* bushes after a considerable dry period.

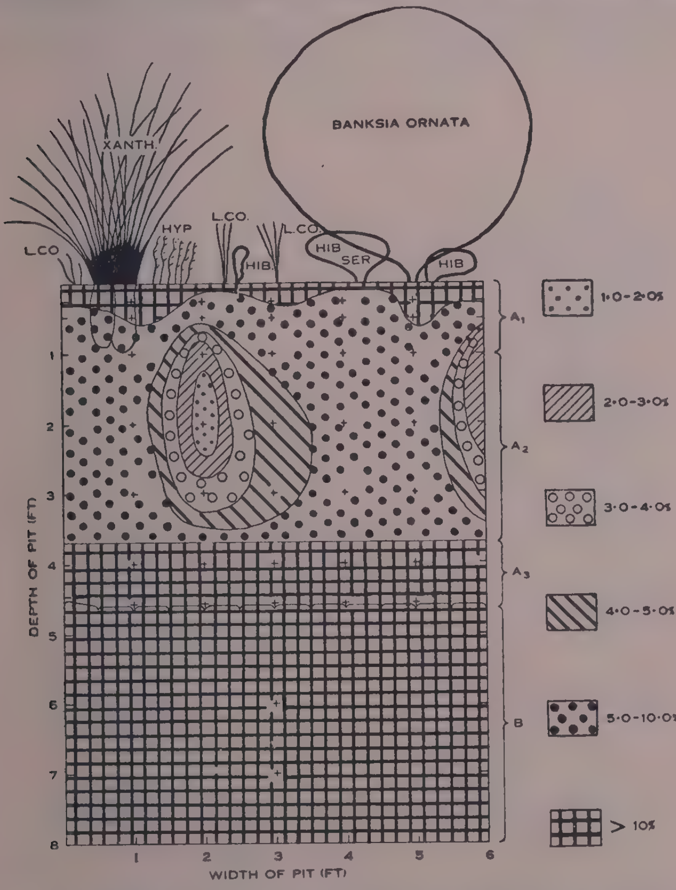

Fig. 4.—Soil moisture pattern under the heath vegetation during a very wet winter (July 8, 1951). The species present were *Banksia ornata*, *Xanthorrhoea australis* (XANTH.), *Hibbertia stricta* (HIB.), *Hibbertia sericea* (HIB. SER.), *Lepidosperma laterale* (L.CO.), and *Hypolaena fastigiata* (HYP.).

Although there was a considerable amount of rainfall interception and stem-flow in *Banksia ornata*, most of the rainfall reached the soil, whereas little more than half reached the soil under *Xanthorrhoea australis*. The rest was either held by the fragments of resin between the leaf-bases of this species or evaporated from the leaves.

If the heavy showers responsible for the distribution pattern shown in Figure 2 fell during midsummer, the high evapotranspiration rapidly utilized all the rain which was stored in the soil and the soil moisture picture returned to that illustrated

in Figure 1. On the other hand. if the showers fell during early autumn when the evapotransporation was much lower than in summer, they created a reserve of soil moisture which lasted until the next rain.

As the frequency of rain increased with the approach of winter, the moisture front moved rapidly through the dry sand. wetting the soil immediately above it to near its field capacity. Nevertheless. the rain-shadows and the zones of accumulation

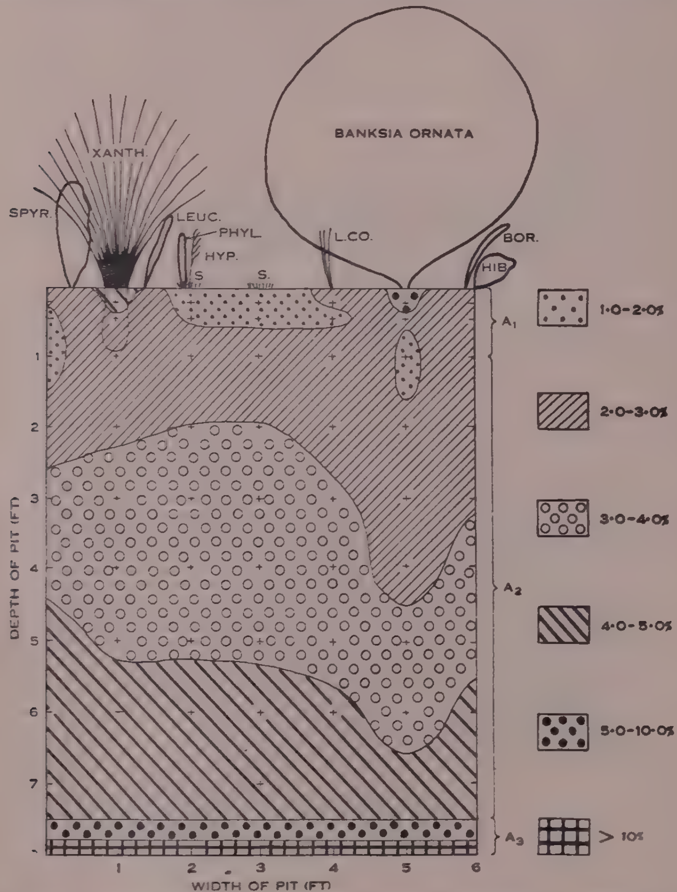

Fig. 5.—Soil moisture pattern under the heath vegetation as spring progresses (Sept. 28, 1951). The species present were *Banksia ornata*, *Xanthorrhoea australis* (XANTH.), *Spyridium subochreatum* (SPYR.), *Hibbertia stricta* (HIB.), *Phyllota pleurandroides* (PHYL.), *Leucopogon costatus* (LEUC.), *Boronia caerulescens* (BOR.), *Schoenus tepperi* (S.), *Hypolaena fastigiata* (HYP.), and *Lepidosperma laterale* (L.CO.).

observed in Figure 2 were always present. Dry pockets with soil moisture even below 1 per cent. persisted well into the winter period around the periphery of plants of *Banksia* and *Xanthorrhoea*. The centres of water concentration were always immediately below the stock and trunk of *Xanthorrhoea* and *Banksia* respectively, with that under *Banksia* invariably showing the higher concentrations (Fig. 3).

Even during a very wet winter when a perched water-table (moisture 16–23 per cent.) was formed at the junction of the clay subsoil with the sand, dry pockets persisted in the A_2 horizon under the periphery of the two species (Fig. 4). Lateral movement of water within the sand was negligible.

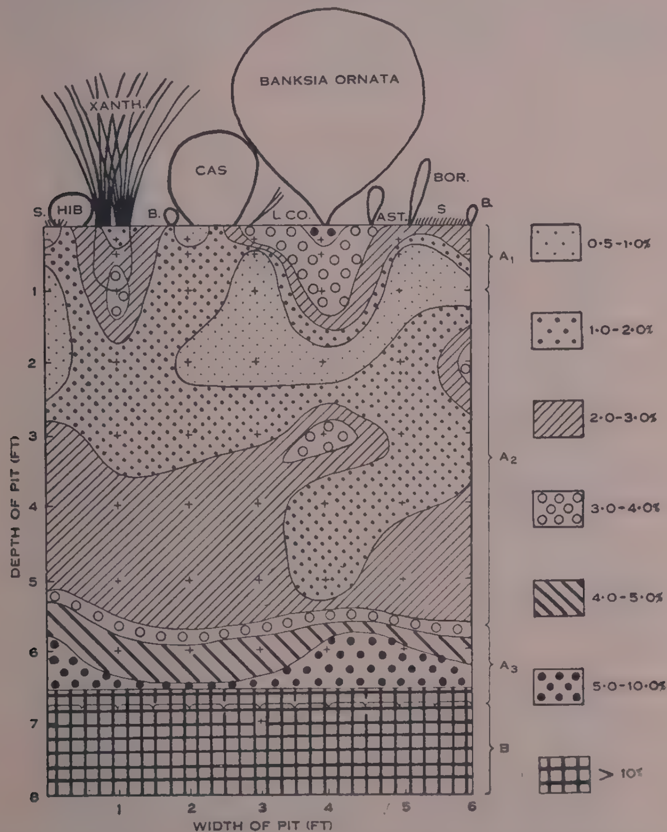

Fig. 6.—Soil moisture pattern under the heath vegetation at the beginning of summer (Dec. 13, 1951). The species present were *Banksia ornata*, *Xanthorrhoea australis* (XANTH.), *Casuarina pusilla* (CAS.), *Hibbertia stricta* (HIB.), *Boronia caerulescens* (BOR.), *Baeckea ericaea* (B.), *Astroloma conostephioides* (AST.), *Lepidosperma laterale* (L.CO.), and *Schoenus tepperi* (S.).

The frequency and, to a certain extent, the intensity of the showers of rain usually decreased as spring progressed. As evapotranspiration became more important there was a steady decrease in the soil moisture from the surface downwards (Figs. 5 and 6). The dense shade underneath the larger bushes maintained there a higher soil moisture content in the top 3–6 in. of soil. If a shower of rain fell, the striking moisture patterns which were seen earlier in the year were re-established (Fig. 7).

In most years, the low rainfall and high temperature of summer eventually resulted in a soil depleted of moisture. A stage in this process is indicated in Figure 8,

where, after a fortnight of maximum daily temperatures near or over 100°F, the top 4 ft of the soil had fallen to a level near its permanent wilting point, while the rest of the sandy A horizon contained 1–2 per cent. of moisture. The soil, a sand able to store only a small portion of the rainfall, dried very rapidly; the drying-out cycle progressed almost independently of the distribution of the species. Before long, if no rain were to fall, the soil moisture would fall to the permanent wilting point, a situation which is illustrated in Figure 1.

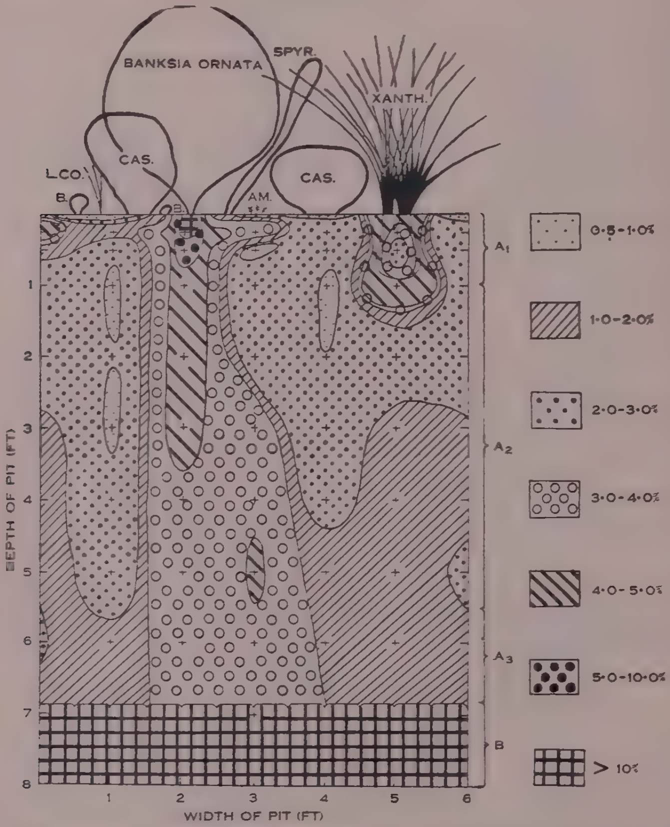

Fig. 7.—Soil moisture pattern under the heath vegetation after heavy rains during spring (Nov. 7, 1950). The species present were *Banksia ornata*, *Xanthorrhoea australis* (XANTH.), *Casuarina pusilla* (CAS.), *Spyridium subochreatum* (SPYR.), *Baeckea ericaea* (B)., *Lepidosperma laterale* (L.CO.), and *Amphipogon caricinus* (AM.).

(*b*) *Analysis of Data*

As 10 of the 24 sampling dates were a few days after heavy showers of rain, it was possible to compare the direct effect of the vegetation on the soil moisture status. Ideally a number of replicated pit-samplings should have been taken at each date but this could not be carried out in practice. However, by means of analysis of variance using the 10 sampling dates as replicates, it was possible to examine the variation in soil moisture directly underneath various species.

The number of inches of rainfall which was stored in the 4 ft of soil (i) beneath the stock of *Xanthorrhoea australis*, (ii) beneath low, small-leafed bushes such as *Casuarina pusilla*, (iii) beneath the stock of, and (iv) beneath the edge of *Banksia ornata*, was calculated. To do this the percentage of moisture recorded at each sampling point was plotted against depth in inches. The area under the curve (percentage moisture × depth) was determined by means of a planimeter and substituted in equation (**1**). The results are illustrated in Table 1. Analysis of variance

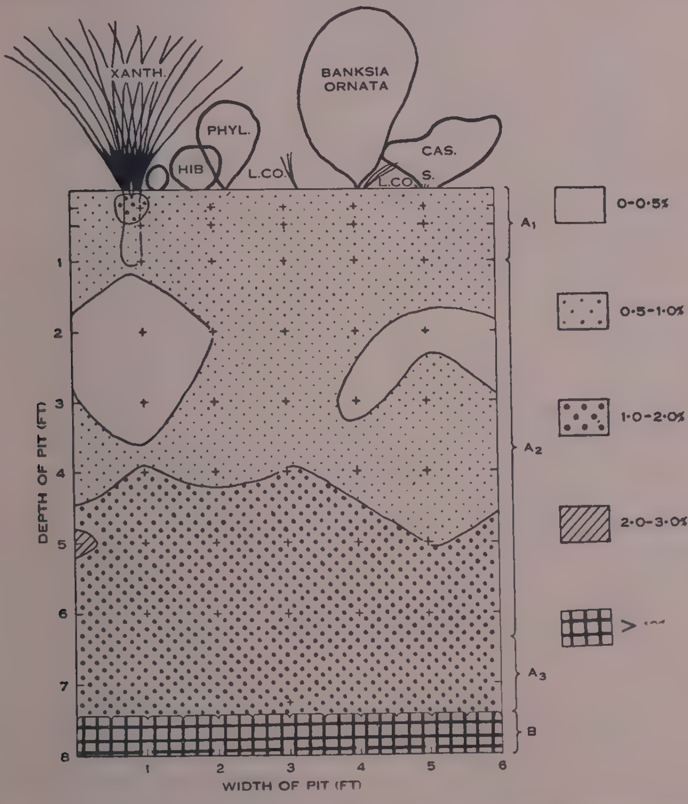

Fig. 8.—Soil moisture pattern under the heath vegetation as summer progresses (Dec. 14, 1950). The species present were *Banksia ornata*, *Xanthorrhoea australis* (XANTH.), *Casuarina pusilla* (CAS.), *Phyllota pleurandroides* (PHYL.), *Hibbertia stricta* (HIB.), *Lepidosperma laterale* (L.CO.), and *Schoenus tepperi* (S.).

showed that the rainfall stored in the soil under any one site was significantly different from that in each of the other sites. This confirms the phenomena of rainfall interception and stem-flow discussed above.

Supplementary data were obtained in February 1955, after rain totalling 1·95 in. had fallen over a period of one week on to soil which was previously at its wilting point for a depth of at least 6 ft. Soil moisture samples were collected from four situations: (i) under *Banksia ornata*, (ii) under *Xanthorrhoea australis*, (iii) under

Casuarina pusilla, and (iv) in open areas between bushes. These four sampling sites were chosen at random within a few yards of each other, the set being replicated

TABLE 1

RAINFALL (IN.) STORED IN THE TOP 4 FT OF SAND AT VARIOUS SAMPLING DATES

Date	Under *Xanthorrhoea australis*	Under *Banksia ornata*	Edge *Banksia ornata*	Under Other Bushes
20. iii.50	1·15	2·64	1·47	0·52
3. vi.50	3·84	3·49	1·33	3·24
8.vii.50	2·94	3·62	2·35	2·48
9. ix.50	2·09	2·37	1·55	1·73
9. x.50	2·32	2·94	1·60	2·23
7. xi.50	1·52	3·24	0·76	1·24
30. iv.51	2·92	2·52	0·76	0·71
17. vi.51	2·89	3·17	1·89	2·78
8.vii.51	4·63	5·12	2·80	3·82
9. ix.51	2·36	3·54	1·59	3·07
Mean	2·67	3·27	1·61	2·18

Significant differences between means: 5 per cent. level, 0·48; 1 per cent. level, 0·64; 0·1 per cent. level, 0·86.

TABLE 2

RAINFALL (IN.) STORED UNDER VARIOUS SPECIES OF HEATH ON FEBRUARY 17, 1955

Measurements were made after recent falls of rain totalling 1·95 in. The soil was at its wilting point before the rain

Replicate Site	Under Open Areas	Under *Casuarina pusilla*	Under *Xanthorrhoea australis*	Under *Banksia ornata*
1	2·03	2·41	0·66	2·76
2	2·00	1·33	1·20	3·07
3	2·76	2·11	1·42	2·73
4	2·73	0·35	1·91	2·00
5	1·24	0·35	2·15	3·23
6	0·84	1·15	2·45	2·69
Mean	1·93	1·28	1·63	2·75

Significant differences between means: 5 per cent. level, 0·95; 1 per cent. level, 1·32.

at six random positions throughout the stand of heath. The rainfall stored at each sampling site was calculated as above and is shown in Table 2.

Analysis of variance revealed that the soil moisture underneath the stock of *Banksia ornata* was significantly different from that under *Casuarina* and *Xanthorrhoea*. Application of a *t*-test on the data for the open areas and for *Banksia* showed them to be just significantly different at the 5 per cent. level. Again rainfall interception and stem-flow in *Banksia ornata* produced a significant increase in the soil moisture. However, the variation between replicates was so great that it was impossible to show any subtle differences between the other sites even if they were present.

IV. Discussion

When rain falls on the heath vegetation a large percentage of it must strike some part of a plant, for as much as 70 per cent. of the ground is covered by vegetation (Specht 1953). As Specht and Rayson (1957*a*) have shown, many of the species are leptophylls, i.e. possess very small leaves. Much of the rain passes between these leaves to the soil; the rest is retained either as droplets within the axils of the leaves etc., or as a film over the leaves and stems. The dense layer of leaf litter under these bushes also intercepts considerable rain, though no estimations have been made of the percentage of total rain which is thus retained and evaporated. Observations in the soil under leptophyllous species indicated that soil moisture was significantly less there than under the broad-leafed *Banksia* and *Xanthorrhoea*. Probably because there were insufficient replicates these sites were not shown to differ significantly from bare areas in the heath where no interception of rainfall occurred. Nevertheless, although the decrease in rainfall by interception on foliage and litter of the leptophyllous species is a distinct possibility, stem-flow appears to be negligible.

However, marked rainfall interception and stem-flow produce rain-shadows and centres of concentration under the larger, nanophyllous bushes of *Banksia ornata* and *Xanthorrhoea australis*. Quite a considerable portion of the rain which strikes the leaves of *Xanthorrhoea* may be lost directly by evaporation. Much of the rain which falls on *Banksia ornata* finally reaches the soil. In all, an irregular pattern of soil moisture results and persists throughout much of the year.

These patterns become more and more important as the heath ages. *Xanthorrhoea* grows very rapidly from its underground stock after a fire and soon dwarfs the other species. *Banksia ornata* regenerates from seed: its growth is slow, but, after ten years of growth, it is much taller than the other species. More and more rain is intercepted by these large, nanophyllous bushes at the expense of the leptophyllous undershrubs which are gradually killed.

V. Acknowledgment

The author wishes to thank Professor J. G. Wood for his advice and encouragement throughout this project.

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DARK ISLAND HEATH (NINETY-MILE PLAIN, SOUTH AUSTRALIA)

V. THE WATER RELATIONSHIPS IN HEATH VEGETATION AND PASTURES ON THE MAKIN SAND

By R. L. Specht*

[*Manuscript received April* 23, 1957]

Summary

Heath vegetation shows a major flush of growth during the mediterranean-type summer season, a time when calculations of the soil moisture storage by the techniques of Thornthwaite (1948) or Prescott, Collins, and Shirpurkar (1952) indicate that severe drought conditions should occur. Monthly observations on the moisture status of the Makin sand under heath vegetation and, for comparison, under various pastures are therefore recorded.

The problems of obtaining an accurate water balance-sheet for such a heterogeneous vegetation as the heath are discussed. Difficulties in the use of the various techniques for measuring soil moisture in sand, which has a low pF of 1·85 at field capacity, are enumerated.

The following relationships were found between the evapotranspiration index ($I_{tr} = E_{tr}/E_w{}^{0\cdot75}$) and the available water (W). These data were calculated for 6 ft of sand.

(i) Heath vegetation (10–14 years old) . . log $(2\cdot4-I_{tr}) = 0\cdot420-0\cdot0383\ W$
(ii) Heath vegetation (burnt) . . . . log $(2\cdot4-I_{tr}) = 0\cdot461-0\cdot0360\ W$
(iii) *Oenothera odorata* Jacq. pasture . . . . . . log $(2\cdot4-I_{tr}) = 0\cdot395-0\cdot0269\ W$
(iv) *Medicago sativa* L. pasture . . . . log $(2\cdot4-I_{tr}) = 0\cdot390-0\cdot0270\ W$
(v) *Ehrharta calycina* Sm. pasture . . . . . . log $(2\cdot4-I_{tr}) = 0\cdot400-0\cdot0339\ W$

From these equations the mean monthly quantities of rainfall which may be stored in 6 ft of sand under the various treatments described were calculated. Drought conditions are shown to occur in December and January, but are relieved in the later months of summer. Even if the stored moisture below 6 ft is considered, the soil moisture status would be expected to be just sufficient to maintain the vegetation in a "dormant" state, and yet the major growth of the heath vegetation occurs at this time.

The calculated mean annual values of I_{tr} range from 0·53 to 0·60 for these perennial communities. Close approximations to the actual soil moisture status can be obtained by substituting these values for K in Prescott's formula for potential evaporation, i.e. $E_{tr} = K \times E_w{}^{0\cdot75}$.

Supplementary data on transpiration, growth, and the root systems of the pastures are also included.

I. Introduction

In the first paper of this series, Specht and Rayson (1957*a*) discussed phenological data for the heath vegetation in relation to some general factors of the environment. The flush of growth was quite out of phase with the present climate. Unlike the vegetation of all other areas with mediterranean-type climates where a major growth flush during springtime is followed by a period of dormancy during the hot, dry summer, the dominant species of the heath vegetation of southern Australia grow during the summer.

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If the techniques of Thornthwaite (1948) or Prescott, Collins, and Shirpurkar (1952) are applied to the meteorological data for Keith, the reserves of soil moisture built up during the mediterranean winter are shown to be depleted by the onset of summer in December (see Specht and Rayson 1957*a*, Fig. 2). Thornthwaite and Mather (1954) stressed the point that the potential evapotranspiration, which was used to estimate the soil moisture, "appears to be independent of soil type, crops, or mode of cultivation". Their evidence undoubtedly supports their statement that the potential evapotranspiration is independent of crop, but it appears that they have been unfortunate in their selection of species. Evidence produced by Prescott and Thomas (1948) and Butler and Prescott (1955) indicates that quite a wide range of potential evapotranspirations can be expected for different types of vegetation. These authors state that values of the ratio $E_{tr}/E_w^{0\cdot75}$ varying from 0·8 to 2·4 may be found, provided there is an abundant supply of moisture in the soil. If the supply of soil moisture falls the ratio will also fall below these values. However, even if the lowest ratio of 0·8 is used for the calculation of the soil moisture, it can be shown that there was still no reserve of water left in the soil by December when the growth of the heath commenced and when no recharge could be expected until April.

Such a situation occurs in the chaparral of California (Cooper 1922) and the garigue and maquis of the Mediterranean coast (Braun-Blanquet 1936) where the growth flush occurs mainly in spring. It was impossible to visualize summer growth in southern Australia occurring in the absence of moisture other than that from the erratic summer rains. Monthly observations on the moisture status of the Makin sand firstly under heath vegetation and later, for comparison, under several pasture species were made to investigate this phenomenon. This paper presents the results of these investigations.

II. Techniques

Any investigation which aims to present a water balance-sheet for an ecosystem as complex as that of the heath vegetation is bound to encounter many difficulties. Variations in microclimate (Rayson 1957), soil texture (Aitchison, Butler, and Gurr 1951), soil organic matter, and rainfall interception and stem-flow (Specht 1957) must be considered. The selection of sites exhibiting the least variable microhabitat is important; careful replication is essential to encompass other variations.

Before choosing a technique suitable for the study of the soil moisture in a pure sand it is imperative to examine the soil moisture—pF curves for the various horizons. These were kindly determined by Mr. J. W. Holmes of the Soil Physics Section, Division of Soils, C.S.I.R.O., Adelaide, by means of the pressure membrane apparatus of Richards (1941) and ceramic suction plates. The curves for the grey organic A_1 sand, the yellow A_2 sand, and the sandy clay B horizon are shown in Figure 1. In contrast with the B horizon the pF of the two sands falls very rapidly from the permanent wilting point at pF 4·2 to about pF 2·5 whilst the change in the soil moisture percentage is only 0·9 per cent. and 0·2 per cent. respectively for the A_1 and A_2 horizons. Below a pF of 2·5 the slopes of the curves rapidly decrease and tend to approach pF 1·4 as the sands become saturated with more than 20 per cent. of moisture.

The permanent wilting points at pF 4·2 are 1·2 per cent. and 0·7 per cent. respectively for the A_1 and A_2 horizons. These values were verified by the sunflower technique of Veihmeyer and Hendrickson (1934). The field capacities were determined at approximately 6·5 per cent. and 5·5 per cent. respectively for the two horizons. These levels correspond to a pF of approximately 1·85, a value which agrees with that found by Marshall (1945) for the Winkie sand. This low value for the pF of the sands at field capacity contrasts markedly with that of heavier-textured soils, the field capacities of which are roughly equal to their moisture equivalents at pF 2·7.

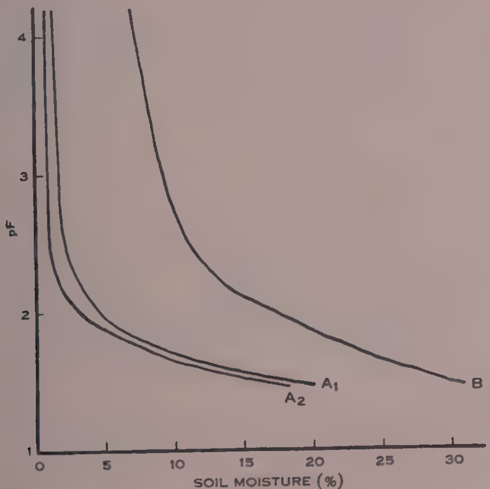


Fig. 1.—Soil moisture–pF curves for the A_1, A_2, and B horizons of the Makin sand.

This exceptional range in pF from permanent wilting point to field capacity makes the selection of a technique to measure changes in soil moisture in these soils very difficult. The gypsum block moisture meter as perfected by Aitchison and Butler (1951) measures the pF of soil water in the range 2·5 to 4·2. As shown above, the soil moisture content of sand changes little within this range. This was further demonstrated in the field when, in ignorance of the results shown in Figure 1, an experiment to record the change in soil moisture under various pastures by means of gypsum block moisture meters was established. Figure 2 shows the field calibration curves for the A_1 and A_2 horizons. The logarithms of the resistance R in ohms of the gypsum blocks (corrected to 20°C) are plotted against the percentage of soil moisture of a sample taken as near as possible to a block of the same pF in an uniform pasture. Some discrepancies are bound to occur even in the short distance between the sample and the gypsum block. More samples are necessary at the drier end of the curve to enable greater accuracy in plotting the calibration graph. Nevertheless, the curves stress the lack of sensitivity of the gypsum block moisture meters to measure the soil moisture over much of the range found in these sands.

The tensiometers of Marshall (1946) and Richards (1949) would be preferable for they are sensitive for the range below pF 2·5, where the greatest change in soil

moisture occurs. Their sensitivity decreases as the permanent wilting point is approached. It would be better to use the tensiometer in conjunction with the gypsum block to enable the complete range of soil moisture from field capacity to permanent wilting point to be studied. However, as they require careful handling and frequent supervision, it would have been unwise to leave them to the mercy of the elements for the 3–4 weeks which elapsed between visits to the experimental area.

The recent development of the neutron scattering technique to measure soil moisture (Belcher, Cuykendall, and Sack 1950; Spinks, Lane, and Torchinsky 1951) may be much more satisfactory. Holmes (1956) has obtained satisfactory calibration curves for this method. However, below 2 per cent. soil moisture the accuracy of the measurements decreases (Holmes, personal communication). In effect, this technique could replace the use of the tensiometer, but would still have to be used in conjunction with the gypsum block moisture meters to cover the whole range of soil moisture in sand.

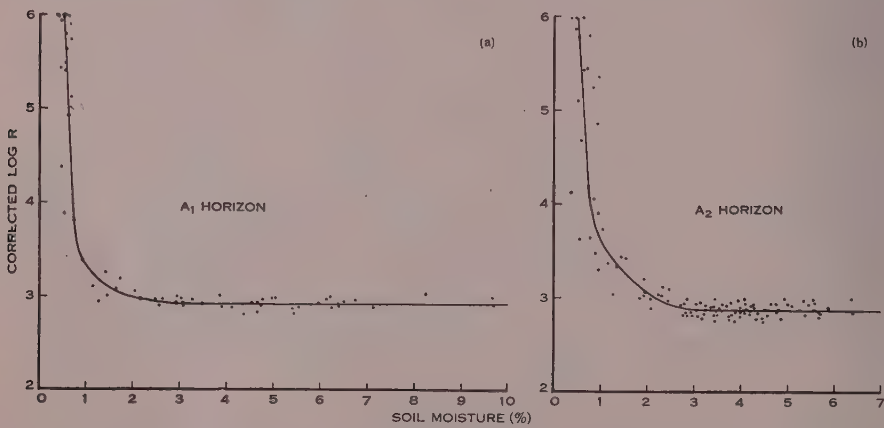


Fig. 2.—Field calibration curve for the resistance of the gypsum block (corrected to 20°C) against soil moisture in the A_1 horizon (*a*) and A_2 horizon (*b*).

The three techniques discussed above all enable continuous records to be made on a series of carefully replicated permanent sites. Because a satisfactory permanent recording technique was not available when the investigation commenced in 1950, gravimetric determinations of soil moisture were made. Later, gypsum block moisture meters were used in an experiment with pasture plants, but the readings were supplemented by gravimetric samples. The small number of replicates—two to six, depending on the circumstances—is open to criticism, but time did not allow further replication. Also, the average depth of sampling was only 6 ft. Although most of the roots are found within this depth, some roots explore greater depths (Specht and Rayson 1957*b*). Deeper sampling is feasible during winter but is impossible during a dry summer as the dry sand tends to fall out of the auger even after careful tamping.

III. Experiments

(a) *Soil Moisture Under Heath Vegetation*

In August 1949, Coaldrake (1951) began a preliminary comparative study of the soil moisture under various plant communities prominent in the upper south-east of South Australia. By means of a soil auger he collected duplicate soil samples for the gravimetric determination of soil moisture at 1 ft intervals down the profile. Two sets of samples were gathered at intervals of 3 weeks from open areas within the vegetation at each site. One of these sites was on the area which was later the centre of the current experiments at Dark Island.

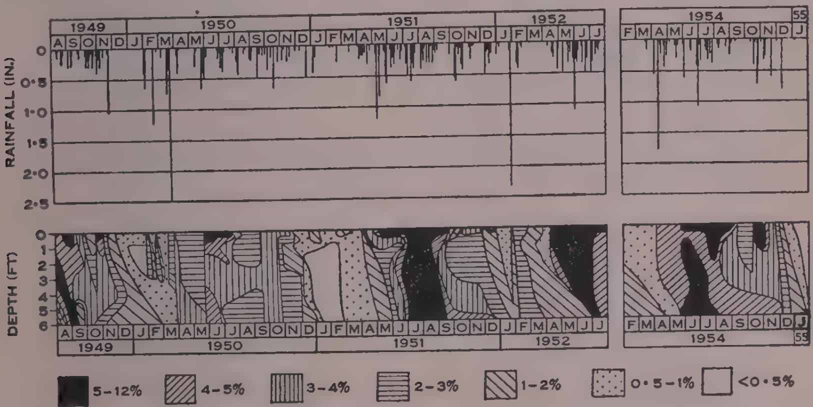


Fig. 3.—Changes in the percentage soil moisture in 6 ft of sand under heath vegetation (10–14 years old) from 1949 to 1954.

Shortly after the completion of Coaldrake's work in January 1950, the study of the soil moisture under the heath vegetation was resumed. Particular emphasis was placed on the variations in the soil moisture contents which are produced by rainfall interception and stem-flow in the various dominant species of the heath (Specht 1957). The soil moisture status at the end of each month was determined gravimetrically by means of samples collected at 1-ft intervals from the face of a pit 6 ft long and 6 ft deep. Further samples at depths greater than 6 ft were collected by means of an auger. As a new site had to be selected each month, irregular depths of sand over the clay subsoil were often found. This made comparisons of the soil moisture status impossible for depths greater than 6 ft. Records of the soil moisture status were compiled by means of the pit technique from February 1950 to March 1952. Shortly after this period duplicated gypsum block soil moisture meters were installed under the heath vegetation. Recordings by this technique were compiled from July 1952 to January 1955. During this period soil samples were occasionally collected as near as possible to the gypsum blocks in order to calibrate them in the field. The results, discussed in Section II above, indicated how ineffective the blocks were to measure the whole range of soil moisture found in a sand. Hence, in 1954, further records were collected monthly by means of the technique used by Coaldrake.

These records were all made on heath vegetation which had not been burnt for 10–14 years. For comparison, data were collected by the technique used by Coaldrake from a stand of heath which had been burnt 6 months previously. Studies were made from September 1950 to April 1951 and from July 1954 to January 1955.

The changes in the percentage soil moistures so obtained from 1949 to 1954 are illustrated in Figure 3.

(b) *Soil Moisture under Various Pastures*

In May 1952 an experiment to compare the soil moisture relationships under several species of pasture which have agricultural potentialities on these deep sands was established. An area of heath where the sand was uniformly 10 ft deep was burnt, ploughed twice, and the remaining *Xanthorrhoea** stocks grubbed out by hand. The land was then harrowed until an even surface was obtained.

Six different pastures replicated six times were laid out in a Latin square design. Each plot was 3 yd square. Pathways of 1 yd separated the plots. The following pastures and rates of sowing were used:

(i)	*Oenothera odorata* Jacq.	4 lb/acre
(ii)	*Ehrharta calycina* Sm.	4 lb/acre
(iii)	*Medicago sativa* L. strain Hunter River ..	4 lb/acre
(iv)	*Trifolium subterraneum* L. strain Bacchus Marsh	4 lb/acre
(v)	*Ehrharta calycina* + ...	2 lb/acre
	Trifolium subterraneum	2 lb/acre
(vi)	Bare ground	—

The seeds were sown with 180 lb superphosphate, 7 lb zinc sulphate and 7 lb copper sulphate per acre. A top-dressing of 180 lb superphosphate per acre was added in each subsequent year. The establishment was excellent except in the case of the mixed pasture where the subterranean clover had a patchy distribution. An attempt was made to reseed these plots with clover seed (4 lb/acre) in August 1952, and again in May 1953, without success. The plots and pathways were maintained as clean as possible by constant weeding. The preferential grazing of the *Ehrharta* and *Medicago* by kangaroos was not satisfactorily prevented until the end of 1953. After this period, these species were able to grow very vigorously in comparison with the first two seasons. No evidence of grazing of *Oenothera* or *Trifolium* was seen.

Before the pastures were sown, six gypsum blocks were installed within each plot at depths of 4, 9, 18, 42, 72, and 120 in., the last depth being just above the clay subsoil. Each block was installed down a separate auger hole placed at random within the plot and at a distance of at least 3 ft from the edge of the plot. Two thermistors were installed at each depth in positions throughout the area.

Readings were made at the end of each month. When field calibrations (Fig. 2) indicated that the gypsum blocks gave accurate results over only a small part of the soil moisture range in the sands, two rows of the experiment were sampled each month for gravimetric determination of the soil moisture.

*Nomenclature follows that used in Part I of this series (Specht and Rayson 1957*a*. Appendix I).

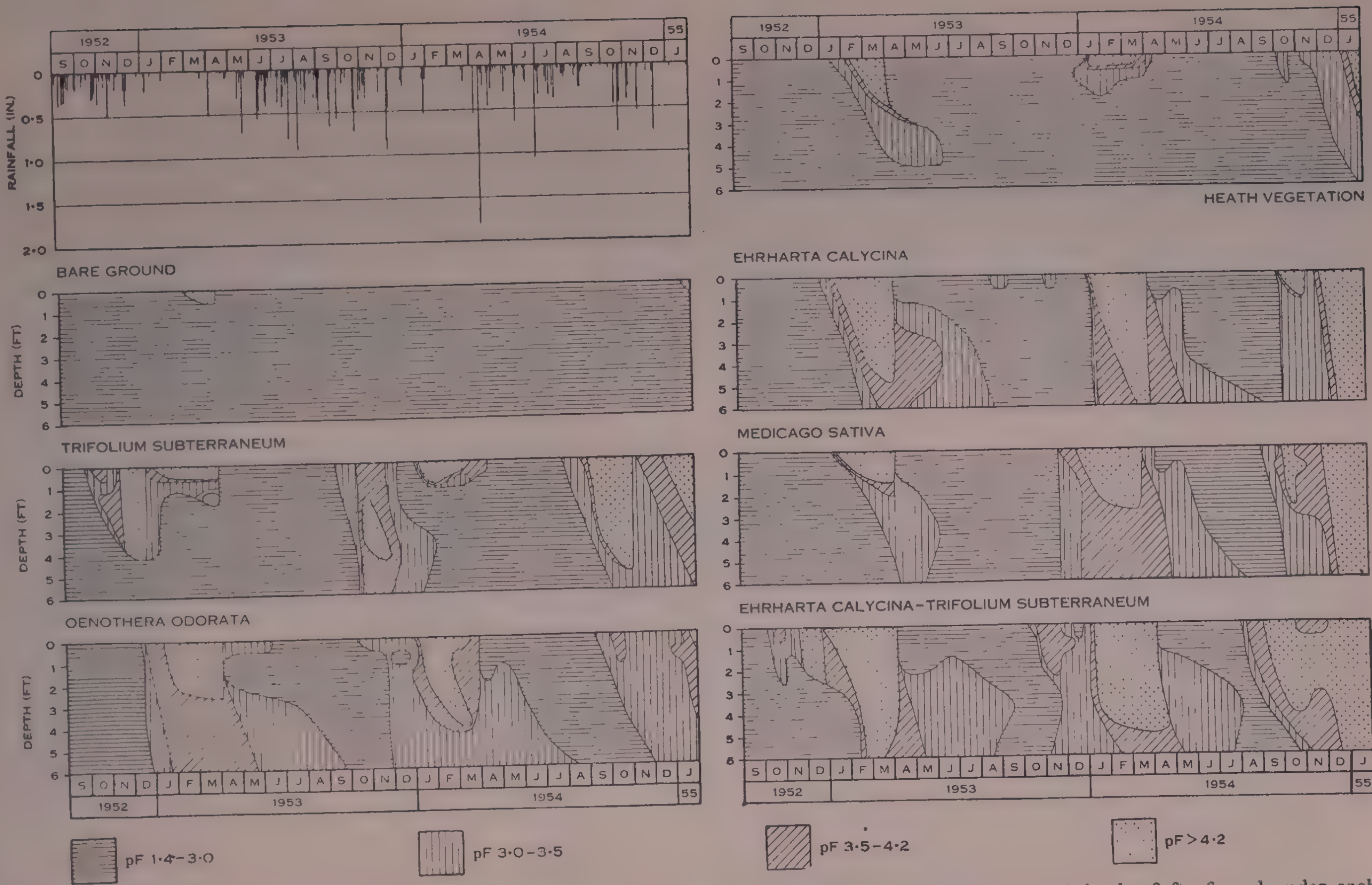


Fig. 4.—Changes in the soil moisture tension (estimated from the data of the gypsum block moisture meter) in the 6 ft of sand under each pasture for the period August 1952 to January 1955.

The changes in the soil moisture tension (as far as it can be estimated by the gypsum block moisture meters) under each pasture are illustrated in Figure 4 for the period August 1952 to January 1955. They may be compared in the same figure with the changes in the soil moisture tension observed under heath vegetation using the same techniques during the same period. Unfortunately, it was found impractical

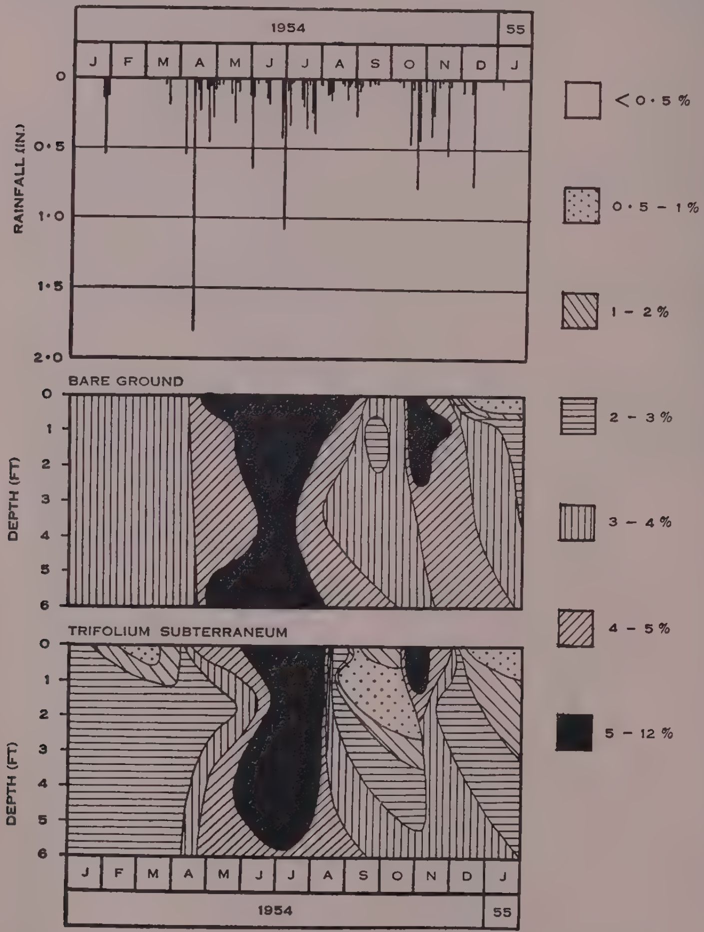


Fig. 5.—Changes in the percentage soil moisture in 6 ft of sand under bare ground and *Trifolium subterraneum* during 1954.

to incorporate the heath vegetation in the experimental design. The soil moisture percentages calculated from the auger samples for the period July 1954 to January 1955 are illustrated for the bare ground and *T. subterraneum* plots in Figure 5.

IV. Interpretation of the Data

The apparent specific gravity, depth, and the percentage soil moisture of each profile examined can be used to estimate the number of inches of rainfall stored in

the soil (see Specht 1957). Only 4·80 in. of rainfall is needed to bring the 6 ft of sand from wilting point to field capacity.* Actually the percentage of soil moisture often fell to a value below the wilting point (*c.* 0·5 per cent.) towards the end of a very dry period. In such a circumstance as much as 5·10 in. of rain may be needed to recharge the soil to field capacity. As soon as the soil is recharged further rain causes water movement into the lower depths of the soil. This occurs almost every winter. A much greater depth of the profile must be examined to reach a depth at which little water penetration is observed; even 10 ft of sand with a storage capacity of 8·00 in. of rain may be too shallow to eliminate drainage in some years. For this reason any month in which drainage was evident was ignored in the investigation.

Evapotranspiration could be calculated, therefore, from the change in the stored rainfall over a period of one month with the addition of the rainfall for that month. The rainfall was measured 2 miles away at the nearest homestead, "Waljena". These records agreed well with the monthly readings which were taken at the experimental site during 1954 by Rayson (1957). As the nearest station recording evaporation was about 100 miles away, the evaporation data were calculated from the 9 a.m. wet- and dry-bulb thermometer readings at Keith (10 miles away) by the formula: Evaporation = 21 × saturation deficit. From all these data it was possible to compare the values of the ratio $E_{tr}/E_w{}^{0 \cdot 75}$ with the available water (the rainfall stored in the soil at the beginning of the month plus the rainfall of that month) by the statistical procedure of Butler and Prescott (1955).

V. Results

The graphs showing the relationship between the evapotranspiration index ($I_{tr} = E_{tr}/E_w{}^{0 \cdot 75}$) and the available water are illustrated in Figure 6 for (i) heath vegetation (10–14 years old), (ii) heath vegetation (recently burnt), (iii) *O. odorata* pasture, (iv) *M. sativa* pasture, (v) *E. calycina* pasture, and (vi) the mixed *E. calycina* and *T. subterraneum* pasture.

The following equations were found to fit the data:

(i) *Heath Vegetation (10–14 Years Old)*.—

$$\mathrm{d}I_{tr}/\mathrm{d}W = 0 \cdot 088\ (2 \cdot 4 - I_{tr}),$$

corresponding to the regression equation for 22 plot-months:

$$\log\ (2 \cdot 4 - I_{tr}) = (0 \cdot 2868 \pm 0 \cdot 0076) - (0 \cdot 0383 \pm 0 \cdot 0042)\ (W - 3 \cdot 4818),$$

with values of I_{tr} ranging from 0·01 to 0·98 and values of W ranging from 0·79 to 6·19 in./month. The terms ±0·0076 and ±0·0042 represent the 95 per cent. fiducial range.

* Wilting points of Makin sand (per cent.): A_1, 1·2; A_2, 0·7. Field capacity of Makin sand (per cent.): A_1, 6·5; A_2, 5·5. Water available between wilting point and field capacity: A_1, 0·87 in.; A_2, 3·93 in.

(ii) *Heath Vegetation* (*Recently Burnt*).—

$$dI_{tr}/dW = 0{\cdot}083\ (2{\cdot}4 - I_{tr}),$$

corresponding to the regression equation for 9 plot-months:

$$\log\ (2{\cdot}4 - I_{tr}) = (0{\cdot}3089 \pm 0{\cdot}0135) - (0{\cdot}0360 \pm 0{\cdot}0012)\ (W - 4{\cdot}2278),$$

with values of I_{tr} ranging from 0·14 to 0·73 and values of W ranging from 2·78 to 6·52 in./month.

(iii) Oenothera odorata *Pasture*.—

$$dI_{tr}/dW = 0{\cdot}062\ (2{\cdot}4 - I_{tr}),$$

corresponding to the regression equation for 13 plot-months:

$$\log\ (2{\cdot}4 - I_{tr}) = (0{\cdot}3346 \pm 0{\cdot}0090) - (0{\cdot}0269 \pm 0{\cdot}0060)\ (W - 2{\cdot}2254),$$

with values of I_{tr} ranging from 0·00 to 0·59 and values of W ranging from 0·61 to 4·52 in./month.

(iv) Medicago sativa *Pasture*.—

$$dI_{tr}/dW = 0{\cdot}062\ (2{\cdot}4 - I_{tr}),$$

corresponding to the regression equation for 10 plot-months:

$$\log\ (2{\cdot}4 - I_{tr}) = (0{\cdot}3250 \pm 0{\cdot}0126) - (0{\cdot}0270 \pm 0{\cdot}0095)\ (W - 2{\cdot}407),$$

with values of I_{tr} ranging from 0·04 to 0·55 and values of W ranging from 0·85 to 4·28 in./month.

(v) Ehrharta calycina *Pasture*.—

$$dI_{tr}/dW = 0{\cdot}078\ (2{\cdot}4 - I_{tr}),$$

corresponding to the regression equation for 9 plot-months:

$$\log\ (2{\cdot}4 - I_{tr}) = (0{\cdot}3256 \pm 0{\cdot}0044) - (0{\cdot}0339 \pm 0{\cdot}0026)\ (W - 2{\cdot}1833),$$

with values of I_{tr} ranging from 0·06 to 0·62 and values of W ranging from 0·80 to 4·40 in./month.

(vi) Ehrharta calycina–Trifolium subterraneum *Pasture*.—

$$dI_{tr}/dW = 0{\cdot}078\ (2{\cdot}4 - I_{tr}),$$

corresponding to the regression equation for 11 plot-months:

$$\log\ (2{\cdot}4 - I_{tr}) = (0{\cdot}3291 \pm 0{\cdot}0126) - (0{\cdot}0338 \pm 0{\cdot}0091)\ (W - 2{\cdot}0982),$$

with values of I_{tr} ranging from 0·01 to 0·58 and values of W ranging from 0·63 to 4·62 in./month. These data were virtually from pure grass plots, for, by the time drainage had ceased, the clover was almost dead.

Tests were then made to examine whether each regression equation was significantly different from the five others. When the regression coefficients were examined, the only pairs of coefficients which were significantly different from each other were:

(1) Heath vegetation (10–14 years old) and the *O. odorata* pasture at the 1 per cent. level of probability.

(2) Heath vegetation (10–14 years old) and the *M. sativa* pasture at the 5 per cent. level of probability.

On the other hand, the means of the ordinate values of log ($2{\cdot}4 - I_{tr}$) showed far less homogeneity than the regression coefficients. The mean for the heath vegetation (10–14 years old) is significantly different from the means for all the other treatments at the 0·1 per cent. level of probability. The mean for the heath vegetation (recently

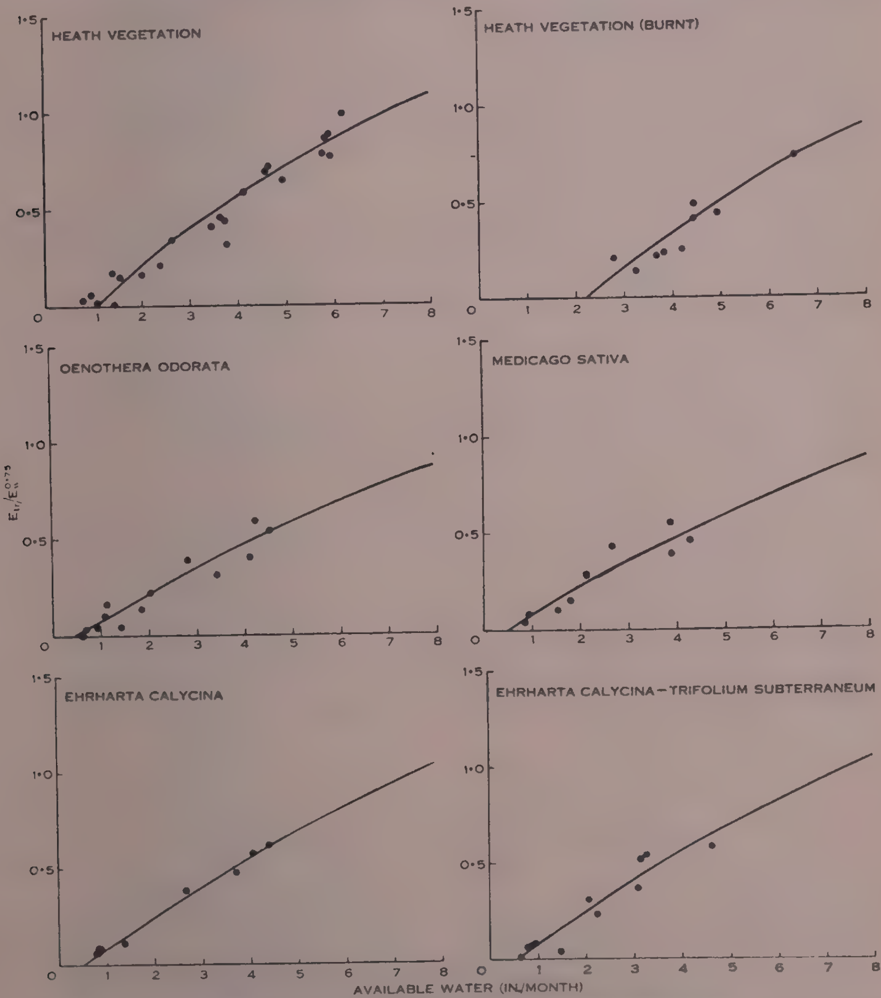


Fig. 6.—Graphs showing the relationship between the evapotranspiration index ($I_{tr} = E_{tr}/E_w^{0{\cdot}75}$) and the available water for six different communities.

burnt) was also significantly different from the means for all the other treatments, but in this case the significance varies from the 0·1 to the 5 per cent. level of probability. The means of all the pastures are homogeneous.

Hence it is apparent that the heath vegetation, whether burnt or unburnt, shows a significantly different amount of evapotranspiration from that of the

perennial pastures. When the available water falls below 3–4 in., the pastures evaporate significantly more water than the unburnt heath vegetation. The converse occurs above the 4-in. water level. Burning of the heath vegetation will significantly reduce the amount of water evaporated. The loss of water from the pastures is then significantly greater than that from the burnt heath for most of the range of available water.

The rates of change of the index of evapotranspiration (I_{tr}) per unit of available water (W) are homogeneous for the heath vegetation and the *Ehrharta* pastures with $\mathrm{d}I_{tr}/\mathrm{d}W$ ranging from $0{\cdot}078\ (2{\cdot}4-I_{tr})$ to $0{\cdot}088\ (2{\cdot}4-I_{tr})$. The *Oenothera* and *Medicago* pastures with $\mathrm{d}I_{tr}/\mathrm{d}W = 0{\cdot}062\ (2{\cdot}4-I_{tr})$ show significantly different rates from the former communities.

Although not sufficient data from the *T. subterraneum* pastures were available to enable a satisfactory plotting of I_{tr} against W, the data suggest that the resultant curve may agree with that found by Butler and Prescott (1955) for a mixed subterranean clover pasture. This annual species evaporated a much greater amount of water than any of the other vegetation types examined. The soil moisture under it was depleted several weeks before that under the other communities examined (Figs. 4 and 5). After the death of this species, rains usually recharged the sand. Evaporation during the summer often reduced the soil moisture at various depths, the dead roots of clover apparently acting as capillary tubes to bring the water to the surface.

The bare ground plots were charged with water up to the field capacity of the sand during the winter months. Spring and summer with higher temperatures and less rainfall produced a fall in the soil moisture from about 5·00 in. at field capacity to 3·00–3·50 in. towards the end of summer. When the surface 2·4 in. was reduced below its wilting point, further loss of water was almost inhibited. This was markedly in contrast with the picture seen under the dead vegetation of subterranean clover, where the barrier of dry surface soil was made ineffective by the presence of the dead roots.

VI. Supplementary Data

(a) *The Transpiration of Some Species of the Heath*

Oppenheimer and Mendel (1939) have pointed out that the techniques used to measure transpiration in the field are crude and are beset with difficulties when results obtained from individual leaves or sprigs are extrapolated to whole bushes or stands. At best, the results can only compare the differences in transpiration between species, and in the seasonal changes in transpiration which occur with any of these species. Absolute values of transpiration cannot be accurately estimated from field measurements.

The rapid-weighing method, by which the loss in weight caused by transpiration from a leaf or shoot is observed over a period of 3 min immediately after the shoot has been severed from the plant, was adopted in this investigation. Terminal shoots were taken from only the sunny side of the bushes. Observations were made on the six major species in the heath at hourly intervals from 7.00 a.m. to 6.00 p.m., at

approximately monthly intervals throughout 2 years. At the same time, hourly values for air and soil temperatures, humidity and evaporation, and light and wind

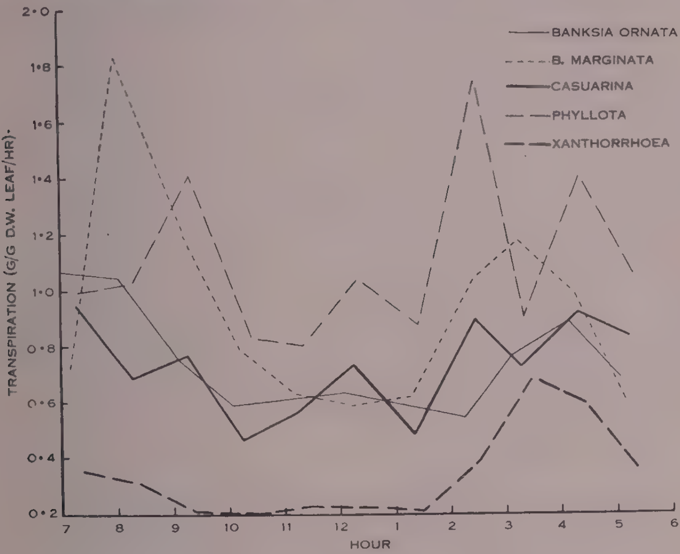


Fig. 7.—Transpiration data for the five major species of the heath on a cloudless summer day—December 1, 1950.

were observed. An attempt was made to record the stomatal aperture by the xylol–ethylene glycol series. However, as the penetration of the solutions was usually obscured by the thick cuticles or dense felts of epidermal hairs of these sclerophyllous species, no satisfactory readings were obtained.

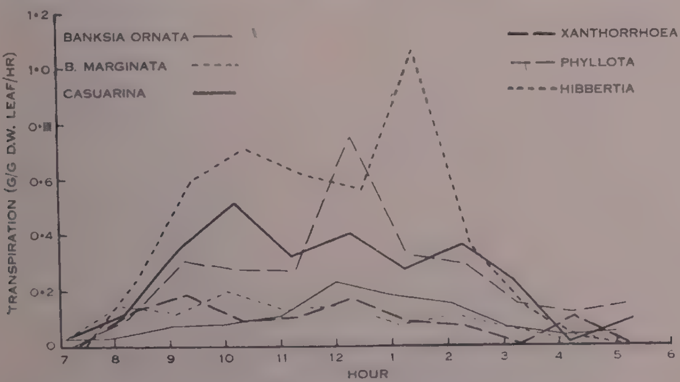
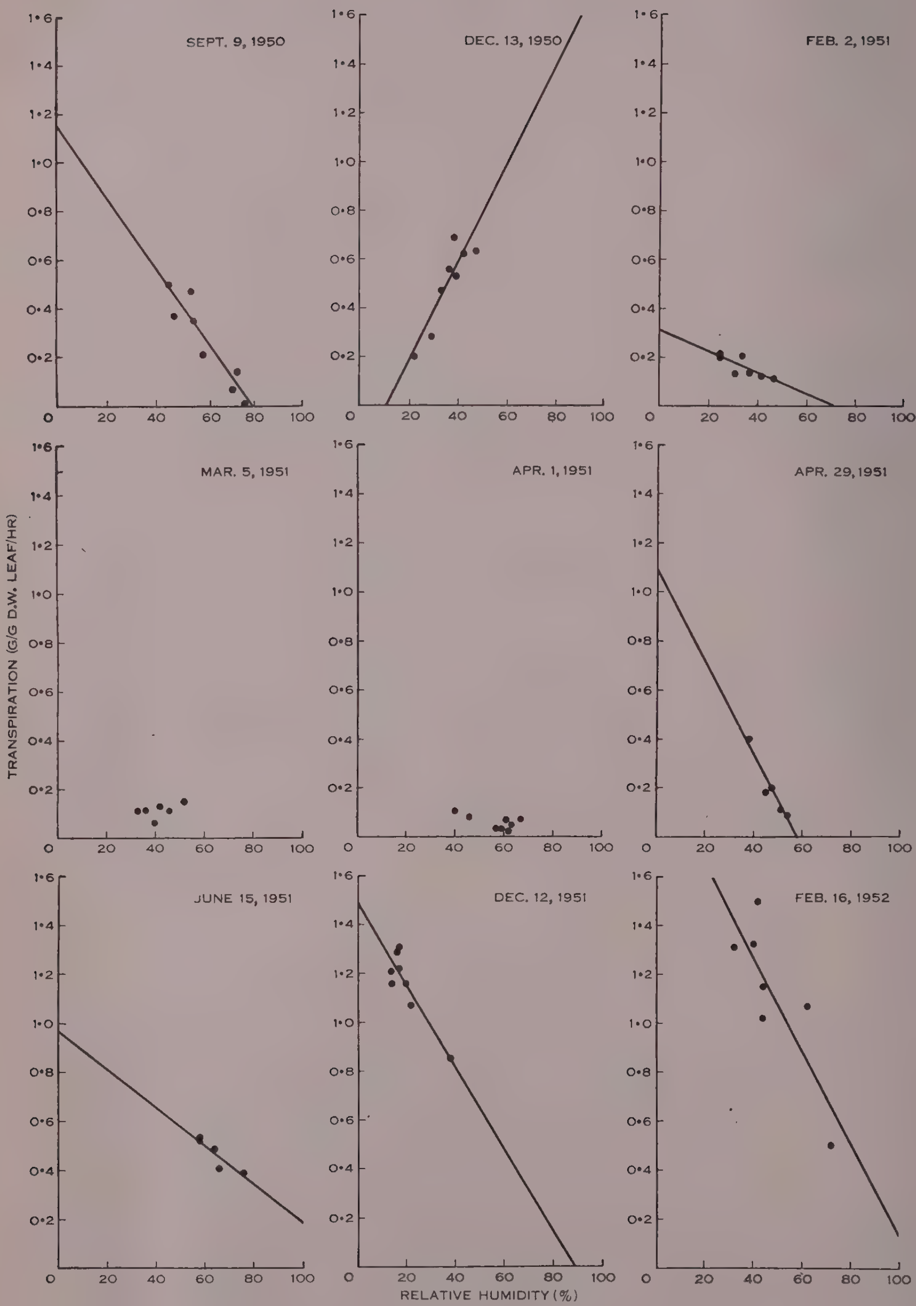


Fig. 8.—Transpiration data for the six major species of the heath on a dull autumn day—April 1, 1951.

The transpiration results, crude and infrequent as they are, serve to indicate daily and seasonal trends in the amount of transpiration from these six species. Figure 7 indicates the daily trends observable during a summer day. The values


SEPT. 9, 1950
DEC. 13, 1950
FEB. 2, 1951
MAR. 5, 1951
APR. 1, 1951
APR. 29, 1951
JUNE 15, 1951
DEC. 12, 1951
FEB. 16, 1952
TRANSPIRATION (G/G D.W. LEAF/HR)
RELATIVE HUMIDITY (%)
0
0·2
0·4
0·6
0·8
1·0
1·2
1·4
1·6
20
40
60
80
100

were high at the beginning and end of the daily records and lower during the hottest part of the day, when apparently the stomata tended to close. Unfortunately, the 7 a.m. to 6 p.m. record only covered a portion of the daylight hours. From other observations, one would expect that the values would also be lower at dawn and dusk, when the temperatures are lower.

As the summer season progressed, the reserves of soil moisture became lower, the levels of transpiration fell, and the higher values shown in the daily fluctuations in Figure 7 became less pronounced.

In winter (Fig. 8) the double humps were no longer apparent; the values of transpiration rose from almost nil at dawn to a maximum during the middle of the day, thereafter the values again fell to almost nil at dusk.

Of course, there were usually more marked variations in the daily curves than those indicated above for the sunny, calm summer and winter days. The transpiration fluctuated greatly from one hour to the next with changing climatic conditions.

If the transpiration was plotted against the relative humidity most of the points were found to lie almost on a straight line. A couple of the points recorded towards midday when the stomata were apparently closing were located away from the line on the zero side. If these points were ignored a regression equation could be derived from the remaining data. The results of the transpiration of *Banksia ornata* on nine separate days are presented in Figure 9. Each day is shown to have a significantly different line. Usually the transpiration increases with decreasing humidity, but the results of December 13, 1950, at the end of a fortnight of very hot, dry weather, indicate the converse picture. The soil moisture had fallen sharply from 1·80 to 0·83 in. in 6 ft of soil during this period. The relative humidity decreased to its lowest value just after midday and then rose. Under such environmental conditions, it is probable that the stomata were open near their maximum at the beginning and end of the day and gradually closed during the day, thus producing this abnormal curve. Unfortunately, however, there are no records of stomatal movements to confirm this statement.

The position and the slope of the curves are probably the result of several factors. The graph of February 16, 1952, is much higher than all the rest. The terminal shoots during February, being young and more mesophytic (Specht and Rayson 1957*a*), probably transpired more water than the older sclerophyllous shoots in the same environment. On this date soil moisture was not limiting, whereas in the previous February (February 2, 1951) the soil was near its wilting point. Consequently, the graph for the latter date is greatly depressed and flattened. After extreme periods of drought the stomata are almost closed and transpiration appears

Fig. 9.—Graphs of the transpiration of *Banksia ornata* against relative humidity on nine separate days. ***, significant at 0·1 per cent. level; **, significant at 1·0 per cent. level; *, significant at 5·0 per cent. level.

Sept. 9, 1950 $T = 1152 - 14{\cdot}47\ H$***	Apr. 1, 1951 not significant
Dec. 13, 1950 $T = 11{\cdot}92\ H - 233$**	Apr. 29, 1951 $T = 1093 - 18{\cdot}99\ H$**
Feb. 2, 1951 $T = 310 - 4{\cdot}26\ H$*	June 15, 1951 $T = 975 - 7{\cdot}92\ H$*
Mar. 5, 1951 not significant	Dec. 12, 1951 $T = 1488 - 16{\cdot}66\ H$**

Feb. 16, 1952 $T = 2038 - 19{\cdot}03\ H$*

to be independent of changes in the relative humidity (March 5 and April 1, 1951). No significant regression equation could be obtained from the information for these two dates.

The other curves indicate that there is a reduction in transpiration with decreasing soil moisture, although other factors may confuse the issue.

As the amount of leaf in the heath vegetation remains almost constant over a period of a year, the new growth being almost balanced by leaf fall, the transpiration records support the results found above by the method of Butler and Prescott (1955). The transpiration is markedly reduced by decreasing soil moisture. Transpiration during periods of extreme drought still occurs because the major species of heath all explore very deep layers of the soil (Specht and Rayson 1957*b*). No observations on the transpiration of the shallow-rooted species of the heath were made during periods of extreme drought; as they are subject to regular summer desiccation of the soil and yet survive, transpiration of these species must cease almost completely.

(*b*) *Growth of the Pastures*

A quadrat 1 ft square was harvested from each of the pasture plots on six occasions during 1954 in order to study the changes in dry weight in relation to changes in the soil moisture (Fig. 4). The results are plotted in Figure 10.

The annual species, *T. subterraneum*, grew steadily from the time of germination and reached a maximum (when the plants were not more than 2 in. tall) in August, after which the soil moisture began to fall rapidly. By the end of October the soil moisture was depleted and most plants died. A period of low rainfall at this time is unusual; in previous seasons, the soil moisture tension had not increased until the beginning of October.

After defoliation during the summer drought, the *O. odorata* pastures resprouted from the stocks or germinated from seeds. The growth of the rosettes increased steadily until August, when flowering stems appeared; these grew rapidly until flowering and fruiting occurred in November and December. This growth was accompanied by a fall in the soil moisture. Dry conditions during January caused extensive defoliation as the soil moisture neared wilting point.

E. calycina showed a growth pattern similar to that of *Oenothera* but with less extensive death of leaves; apparently this species is able to exploit greater depths of soil more easily than *Oenothera*, for the soil moisture was depleted during December.

M. sativa, the least productive of all the pastures, showed little change during winter. As this species grew steadily from August to December the soil moisture fell and was depleted by the middle of December. The plants flowered and fruited during December and early January and were partly defoliated by February. The soil moisture was used slightly faster than under the *Ehrharta* pastures.

These results indicate that the amount of foliage on the pastures usually increases as the soil moisture is reduced. If the pastures were dense, a stagnant atmosphere would be produced in the lower layers where transpiration would be negligible and only the top of the pasture would be actively transpiring. Such a

phenomenon was found by Butler (1951) in a wheat crop. It may occur in the *T. subterraneum* sward but would not be prominent in the discrete tussocks of the other species. In effect, much of the foliage would be actively transpiring. As the transpiring tissue increases while the soil moisture decreases, the slopes of the curves

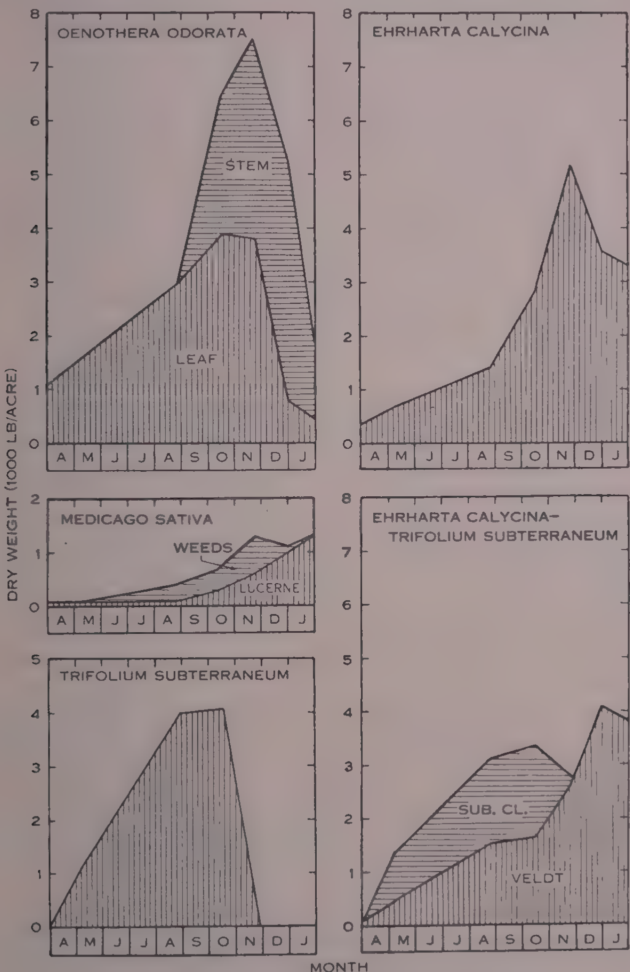


Fig. 10.—Growth curves of the pastures during 1954.

shown in Figure 6 for *Oenothera* and *Medicago* (and to a much less extent for *Ehrharta*) are less steep than those for the heath vegetation, where the foliage remains relatively constant throughout any one year.

(c) *Root systems of the pastures*

Figure 11 depicts the root systems of the species of pasture which were used in the experiment.

T. subterraneum possessed a tap-root which penetrated some 2–4 ft into the sand. In some instances, especially if a decaying root of the former heath vegetation was present, the tap-root descended for about 6 ft. A few small lateral roots were found in the top 3 in. of the surface and fine hair-like laterals were present all the way down the tap-root.

The other three species exploited much more of the profile than the 6 ft examined. *E. calycina* vigorously exploited considerable depths of the soil with its fibrous root system. *M. sativa* possessed a deep-branched or unbranched tap-root system with small laterals especially in the top 6 in. *O. odorata* seedlings possessed a vigorous tap-root with very fine, short laterals. After a few months, a stout lateral system was developed which ramified extensively 2–3 in. beneath the surface of the soil. This root system was similar, on a small scale, to the major species of the heath vegetation (Specht and Rayson 1957*b*).

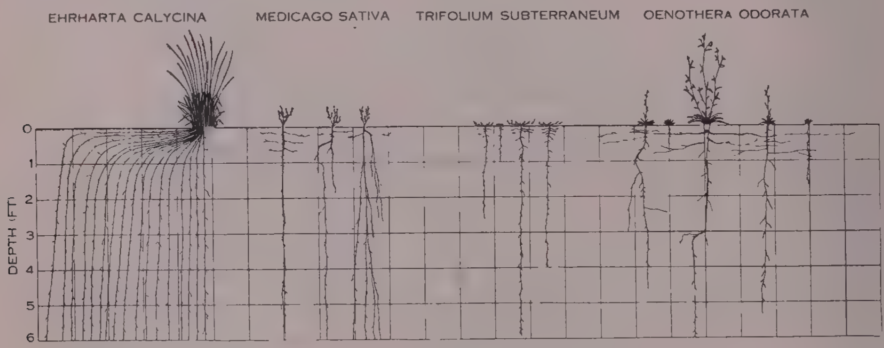


Fig. 11.—Root systems of the four pasture species used in the investigation.

The root system of *T. subterraneum* was the only one of the vegetation types examined which was wholly confined to the top 6 ft of sand. Probably all the others penetrated into the clay subsoil. If so, they did not reduce the soil at that depth to its wilting point, for the gypsum blocks placed at a depth of 10 ft—just above the clay—did not show any major fluctuations during the 3 years of their installation.

VII. Discussion

The graphs showing the relationship between the evapotranspiration index ($I_{tr} = E_{tr}/E_w^{0\cdot75}$) and the available water (Fig. 6), may be used to predict the mean monthly quantities of rainfall which may be stored in 6 ft of sand under the various vegetation types discussed above. One must assume that the soil is saturated with water towards the end of winter (August) and that drainage into the deeper layers of sand or clay subsoil occurs. Field evidence over 7 years supports this assumption. The saturated soil will hold 5·57 in. of rainfall. If this value of stored rainfall (S_1) is added to the mean rainfall (P) of the following month, the available water ($P+S_1$) can be calculated. From the appropriate graph (Fig. 6) the value of I_{tr} can be determined. E_{tr} can then be obtained from the formula $I_{tr} = E_{tr}/E_w^{0\cdot75}$, where E_w is the mean monthly value of the evaporation from a free water surface, or mean monthly

value of $E_w = 21 \times$ saturation deficit. The rainfall retained in the 6 ft of sand at the end of the month can be found by subtracting E_{tr} from the available water, e.g. $S_2 = P + S_1 - E_{tr}$. In this way the values of the stored soil moisture (S_2) can be calculated for each month. The series of calculations for the 6 ft of sand under heath vegetation are shown in Table 1. The mean monthly march of soil moisture and evapotranspiration from the six vegetation types examined is shown in Figure 12.

TABLE 1

CALCULATIONS OF MEAN CLIMATIC DATA FOR UNBURNT HEATH VEGETATION ON 6 FT OF SAND NEAR KEITH, SOUTH AUSTRALIA

Month	S (in.)	P (in.)	$P+S$ (in.)	I_{tr}	$E_w^{0\cdot75}$ (in.)	E_{tr} (in.)	D* (in.)
Jan.	0·89	0·66	1·53	0·11	5·76	0·64	—
Feb.	1·22	0·96	1·85	0·16	3·92	0·63	—
Mar.	1·33	0·84	2·06	0·20	3·61	0·73	—
Apr.	1·89	1·28	2·61	0·31	2·30	0·72	—
May	3·24	2·08	3·97	0·55	1·32	0·73	—
June	4·54	2·01	5·25	0·75	0·94	0·71	—
July	5·57	2·12	6·66	0·93	0·97	0·90	0·19
Aug.	5·57	2·12	7·69	1·06	1·45	1·55	0·57
Sept.	4·95	2·06	7·63	1·05	2·54	2·68	—
Oct.	3·69	1·60	6·55	0·93	3·07	2·86	—
Nov.	2·11	1·26	4·95	0·70	4·05	2·84	—
Dec.	0·87	1·00	3·11	0·40	5·60	2·24	—
Total		17·99				17·23	0·76
Mean				0·60			

* When 5·57 in. of rainfall are stored in 6 ft of sand, the soil has been wetted to field capacity. If further rains are in excess of the monthly evapotranspiration, drainage (D) will occur.

The potential evapotranspiration of Thornthwaite (1948) only occurs when the available water ($P+S$) is at its maximum. In the environment under discussion, such a state is present during July and August, when drainage is apparent. As the mean rainfall for both these months is 2·12 in., the maximum available water is $5{\cdot}57 + 2{\cdot}12 = 7{\cdot}69$ in. The values of I_{tr} under such conditions can be estimated from Figure 6. Unburnt heath therefore shows a maximum value for I_{tr} of 1·06; burnt heath of 0·87; *O. odorata* and *M. sativa* of 0·86; and *E. calycina* of 1·02.

Estimations of the soil moisture by means of these maximum values as suggested by Prescott, Collins, and Shirpurkar (1952) indicate shorter periods of available soil moisture than are actually found in the field. If the more laborious technique used above for the calculation of the soil moisture is not preferred, a close approximation can be obtained by substituting the mean value for the maximum value of I_{tr} in Prescott's formula. The mean values for I_{tr} were calculated as shown in Table 1. The unburnt heath gave a value of 0·60; the burnt heath, 0·63; the

E. calycina plots, 0·58; and the *O. odorata* and poor *M. sativa* plots, 0·57. These values can be used to calculate Prescott's potential evaporation (mean $I_{tr} \times E_w^{0\cdot75}$) and hence the stored soil moisture for each treatment.

It must be emphasized again that these figures refer to only the top 6 ft of sand. Although most of the roots of these perennial plants were confined to this depth, values for the whole profile explored by roots would undoubtedly give figures slightly higher than those indicated. The excess water, shown as drainage, would be utilized during the summer period.

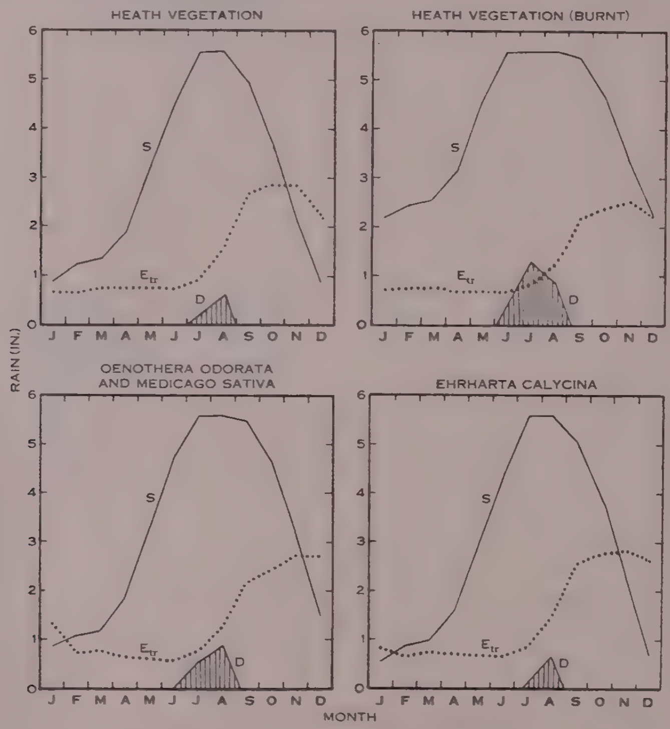


Fig. 12.—Graphs showing the mean monthly values of the soil moisture *S*, drainage, *D*, and evapotranspiration, E_{tr}, which may be expected under the various communities.

In all cases, the stored water fell rapidly during spring until it reached its lowest value during December–January. Burnt areas of heath conserved much water. The *E. calycina* plots lost water most rapidly but not much faster than the unburnt heath, while *O. odorata* and the poor *M. sativa* pastures showed some available moisture well into January. The recharge of the soil moisture, which began in February, was at approximately the same rate for all the treatments which resulted in the soil being reduced to its wilting point. The burnt heath, of course, recharged much more rapidly and caused greater excess drainage. Drainage from the *O. odorata* and poor *M. sativa* plots was almost twice as great as that from the *E. calycina* and heath plots.

Soil moisture under the *T. subterraneum* pastures was probably depleted by the end of October, partially recharged during the summer months after the death of the plants, and rapidly brought to a maximum during the autumn when the seeds germinated.

The evidence suggests that these perennial species use the soil moisture more efficiently during summer than during winter. Reduction in the aperture of the stomata with increasing soil moisture tension probably produced this effect. Thus a portion of the summer showers was conserved and supplemented the drainage which was stored at a depth lower than 6 ft. Nevertheless, January and to a lesser extent December were months of drought for these perennial stands. Partial or total defoliation was apparent in the pastures towards the end of this drought. At the same time, leaf-fall was also at its maximum in the heath vegetation. The soil moisture level during summer was really just sufficient to maintain the vegetation in a "dormant" state; and yet, it supported the major growth flush of the heath vegetation. The problem of the summer growth of the heath vegetation under a limited supply of available water with very small percentages of root system in the B horizon therefore remains unsolved.

VIII. Acknowledgments

The author wishes to thank Professor J. G. Wood of the Botany Department, University of Adelaide, and Mr. J. W. Holmes of the Division of Soils, C.S.I.R.O., for advice throughout the project. Mr. M. Yakhya installed the gypsum blocks and sowed the plots for the study of the soil moisture changes under pasture, but was unfortunately unable to continue the programme because of ill-health. A number of people gave invaluable help in the reading of the gypsum block moisture meters. Miss Leonie Sherwood prepared several of the diagrams for publication.

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THE HIGH MOUNTAIN VEGETATION OF AUSTRALIA

By A. B. Costin*

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Summary

An account is given of the high mountain vegetation of the Australian Alps.

This vegetation is naturally defined as that situated above the level of the winter snow-line (4500–5000 ft); it occupies an area in south-eastern Australia of about 2000 sq. miles.

The high mountain environment can be divided into subalpine and alpine tracts, on the basis of average duration of the winter snow cover and related effects. Relevant climatic data are given, together with information on physiography, geology, flora, fauna, soils, and land use.

The plant communities identified earlier in the Snowy Mountains area are found to provide a generally satisfactory basis for the rest of the high mountain areas. The various fjaeldmark, alpine herbfield, sod tussock grassland, heath, subalpine woodland, and bog and fen alliances are enumerated, with details of distribution and variation in Australia and comparisons with homologous vegetation in Europe.

Five broad ecological types of high mountain are recognized and the characteristic associations of communities are described.

Almost all of the Australian high mountain vegetation has been modified by land use. Few of the existing communities are regarded as stable and the direction of change will depend largely on how they are henceforth managed by man.

I. Introduction

The high mountain vegetation of the Australian mainland (above *c.* 4500–5000 ft) occupies an area of about 2000 sq. miles: *c.* 1000 sq. miles in the south-east of New South Wales, *c.* 140 sq. miles in the Australian Capital Territory, and *c.* 870 sq. miles in Victoria (Fig. 1).

Individual areas, particularly the Snowy Mountains and Bogong High Plains, have been studied in varying detail and many botanical collections have been made (e.g. Maiden 1894, 1898, 1899; McLuckie and Petrie 1927; Morris 1929; Byles 1932; Pryor 1939; Joint Scientific Committee 1946; Turner and Fawcett 1946 et seq.; Garnet 1948; Willis 1948; Morland 1949, 1951; Newman 1953, 1954, 1955; Patton 1953; Wakefield 1953; Costin 1954, 1957; Durham 1956; Taylor 1956) but to date no studies have been made of the Australian high mountain vegetation as a whole. The present paper attempts to meet this need (cf. Costin 1955*b*). Subsequent papers in this series will discuss current soil and vegetation trends, the relationships of the soils and vegetation to land use, and optimum multi-purpose management.

II. The High Mountain Environment in Australia

The high mountain environment is naturally defined as that situated above the winter snow-line, the latter approximating to the upper limit of montane wet

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sclerophyll forest, where the ground is usually snow-covered continuously for not less than one month of the year. The level of the winter snow-line varies from about 4500–5000 ft in Victoria to 5000–5500 ft in New South Wales and the Australian Capital Territory. Subalpine conditions exist where the ground is normally snow-covered continuously for about 1–4 months of the year; this approximates to the range of the snow gum, *Eucalyptus niphophila*. Above the tree-line of snow gum (at 5500–6000 ft in Victoria and 6000–6500 ft in New South Wales), where the ground is snow-covered for longer periods, alpine conditions occur. Although montane,

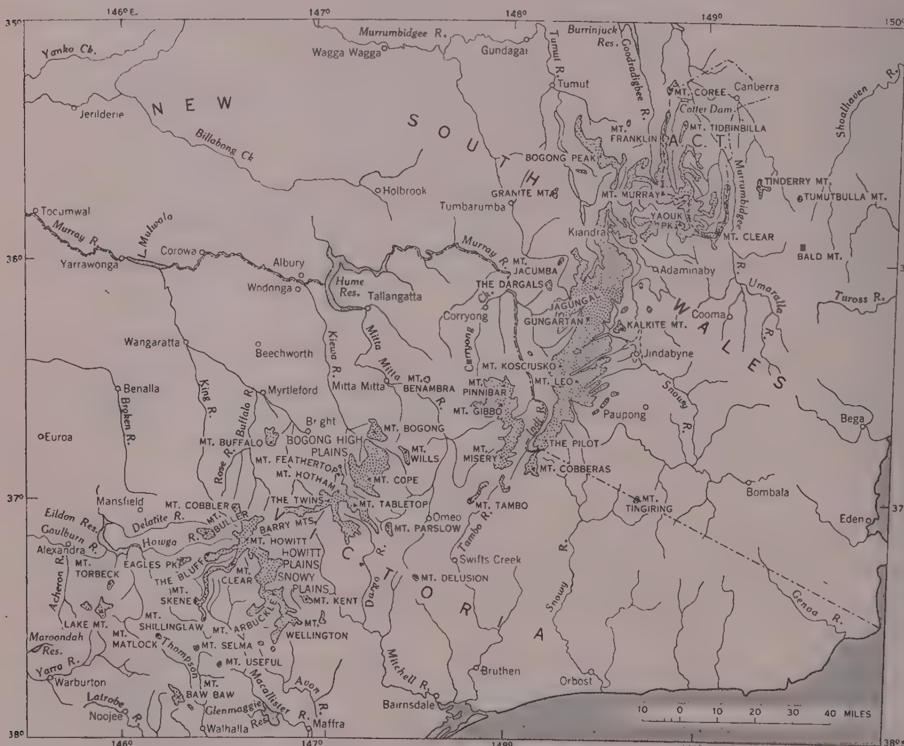

Fig. 1.—Map of Australian Alps, showing land above 4,500 ft.

subalpine, and alpine conditions are generally zoned according to elevation, this is by no means always the case. Cold air drainage, with temperature inversions in valleys and upland flats situated at montane levels, frequently produces high mountain conditions. Much of the so-called "high plains" country of Victoria and New South Wales is of this type.

Except for the Snowy Mountains and Bogong High Plains, where various meteorological data are being accumulated in conjunction with hydroelectric development, quantitative information on the high mountain climate is difficult to obtain.

Often blowing with gale to hurricane force, the prevailing north-westerly to south-westerly winds are associated with most of the precipitation, which falls with a relative winter incidence. In winter the precipitations are mainly in the form of snow, and in summer in the form of heavy thunderstorms.

In the subalpine tract average annual precipitations vary from about 30–80 in., and the number of "rain days" from about 120–140. In the alpine tract, precipitations are higher (from about 70–120 in. p.a., with about 130–150 rain days) and the period of snow cover is increasingly greater, until in local snow-patch situations it persists for most of the year.

Mean monthly maximum temperatures rise to about 60–75°F in midsummer in the subalpine tract, and probably about 50–60°F in the alps. The corresponding mean monthly minima fall to about 25–30°F and to less than 25°F in midwinter, and do not exceed freezing point for about 6 and 6–8 months of the year respectively. During the snow-free months, however, when there is often a regular alternation of warm days and freezing nights, daily temperatures are considerably higher and lower than the monthly means would indicate, the diurnal range not infrequently approaching 50°F or more. This is especially so in the broad, subalpine valleys, where cold air drainage and temperature inversions are severe.

Meyer ratios in the subalpine and alpine tracts vary from about 400 to 1000 and 1000 to 1500 respectively. However, as pointed out elsewhere (Costin 1954), this type of moisture index fails to provide adequately for limiting temperatures during the colder months, and under snow conditions is of only limited application. Indeed, during the winter months it is doubtful if many meteorological data are of great ecological significance, owing to the blanketing effect of the snow.

Geologically, the Australian Alps show considerable variation, all of the main rock types such as acid granites, slates, basalt, and limestone being represented. In contrast to Europe, however, the high mountain soils and vegetation are not strongly differentiated according to rock type. Locally, relatively eutrophic and oligotrophic plant communities and soils do occur (e.g. fens and bogs), but as a generalization it can be stated that similar communities and soils occur on different rocks. Thus, of the eight well-defined soil groups—alpine humus soils, lithosols, gley podzols, acid marsh soils (silty bog soils), snow-patch meadow soils, bog peats, poor fen peats, and humified peats—the alpine humus soils develop as the climatic climax on all kinds of parent material. These soils, although strongly acid and base-unsaturated, are neither peaty nor podzolized, and appear to be stabilized against further leaching owing to a small but significant return of bases and mineral matter by decomposing herbs and earthworm activity (cf. Costin, Hallsworth, and Woof 1952). This is in contrast to the mountain soils of Britain and Scandinavia which are considered to be undergoing progressive base depletion leading to mor formation and further restriction of arctic-alpine species (see Pearsall 1950). Moreover, compared with the high mountains of Europe, where the surfaces are predominantly peaty or rocky, the Australian Alps are in the nature of soil mountains (Costin 1955*b*). This stronger soil development in Australia is related to the milder glacial history, the gentler slopes, the favourable climate for soil weathering, and the unusually vigorous biological conditions in the soil (Costin, Hallsworth, and Woof 1952).

There is also a broad similarity between the general appearance of most of the Australian high mountain areas, which cannot be explained entirely either in terms of the generally accepted geological history or of present-day conditions. An increasing amount of information is accumulating that not only the Kosciusko area and its environs but also parts of the Victorian Alps were modified by ice action in the Pleistocene period (Carr and Costin 1956); such a similarity of glacial history would contribute to the similarity of land forms and vegetation shared by many of these high mountain areas.

Notwithstanding a degree of endemism and geographic variation from south to north, the high mountain flora and fauna are remarkably uniform throughout their range. This uniformity also contributes to the general constancy of the vegetation from place to place.

Land use—involving summer grazing associated with burning, and recurrent bush fires—has been primitive and exploitative in virtually every area of high mountain country in Australia and has impaired its efficiency as a water catchment, often to a serious degree. In places, recent engineering and tourist activity have increased and extended the damage. In view of the unusual susceptibility of the Australian mountains to damage (Costin 1955*a*), problems of catchment conservation are likely to assume major importance unless effective remedial action is taken without delay.

The main occurrences of high mountain country on the Australian mainland are shown in Figure 1. The more northern mountains of the Barrington Tops, New England Plateau, and Bellenden Ker, etc. just fail to qualify as high mountain because of the lack of regular winter snow cover, although small areas of high mountain vegetation are preserved there. Commencing in the Australian Capital Territory, the high mountain country proper extends southwards and south-westwards into New South Wales into the headwaters of the Murrumbidgee and Goodradigbee Rivers, then as the Fiery Range and Snowy Mountains to the Pilot, and to Mts. Cobberas, Gibbo, and Pinnibar in Victoria. Further westwards rise the Bogong High Plains area and the Buffalo Plateau, and south-westwards Mt. Buller and Mt. Stirling with the long arc of mountains stretching from Mt. Cobbler through Mt. Howitt to The Bluff, from which a still more southerly arm extends through Mts. Clear, Skene, and Shillinglaw in the direction of the Baw Baw Plateau. Southwards from the Bogong area are the Dargo High Plains, and from Mt. Howitt the extensive series of high plains including Howitt Plains, Bryce's Plains, Snowy Plains, Holmes Plain, Bennison Plains, and finally the Big Plain near Mt. Wellington. Numerous smaller areas of high mountain country are also shown in Figure 1. Further consideration of these areas will be deferred until the distribution of the vegetation is discussed. At this stage it will suffice to point out the relatively gentle slopes of the Australian high mountains compared with most other high mountain environments overseas, and the importance of the high plains type of topography.

III. The High Mountain Plant Communities

Earlier ecological work in the Monaro Region of New South Wales (Costin 1954) led to the recognition of the major floristic and structural groups (alliances,

subformations, and formations, after Beadle and Costin 1952). This work has been found applicable to the rest of the high mountains of the Australian mainland. For the most part the associations are also the same, although at this level there is still a good deal of information to be added.

The climax high mountain communities of the Australian mainland are listed in Table 1, with summarized environmental data. The alliances and structural units can be regarded as more or less complete, but the list of association dominants will require some amplification to accommodate those few additional associations which occur outside the Monaro Region. (For further details and for illustrations of climax communities, see Costin 1954).

The fjaeldmark communities of the *Epacris petrophila–Veronica densifolia* alliance are virtually restricted to the exposed alpine cols and summits of the Kosciusko area. In one or two places in the Bogong High Plains area, namely, Mt. Nels, Mt. Bogong, and the Feathertop Razorback, *Ewartia nubigena* and *Helipterum incanum* var. *alpinum* occur as this wind-exposed type of fjaeldmark, but it is not known precisely to what extent this condition has developed as the result of accelerated erosion. This form of fjaeldmark vegetation is typical of windswept, subglacial situations such as Macquarie Island, Iceland, and the Braeriach Plateau in Scotland (cf. Watt and Jones 1948; Taylor 1955): in these areas the moss *Rhacomitrium lanuginosum* Brid. is usually characteristic.

Whereas the above-mentioned fjaeldmark communities are determined primarily by conditions of exposure to cold winds, those of the *Coprosma pumila–Colobanthus benthamianus* alliance are determined mainly by exposure to cold. They are usually restricted to the rocky sides and upper margins of snow patches, which do not receive melt-waters from the snow. These habitats are consequently relatively dry during the snow-free period, although they are subject to strong cold and large temperature fluctuations on account of their proximity to the snow-patch. Although this alliance develops only in the Kosciusko area and does not extend to the Victorian Alps, it is interesting to record the presence of one of the characteristic dominants, *Coprosma pumila*, growing in herbfield vegetation near the stony summits of Mt. Lovick and The Bluff. The same species again occurs on the Baw Baw Plateau, but in this instance in association with *Sphagnum* bogs. This type of fjaeldmark vegetation is another subglacial and peri-nival community, in this instance developed in association with permanent or semi-permanent snow or ice and exposed to cold and drought during the brief snow-free period but lacking the extreme exposure to strong winds experienced by the former fjaeldmark alliance. In other countries this type of vegetation ascends higher than any others. In Scandinavia a few flowering plants are characteristic of the higher levels (e.g. *Ranunculus glacialis* L., *Luzula* spp., *Salix* spp.), but as the permanent snow-line is approached cryptogams become completely dominant. On the Continent, on the other hand, the phanerogams do not completely disappear.

The short alpine herbfields of the *Plantago muelleri–Montia australasica* alliance are best developed in snow-patch situations which during the snow-free season are irrigated by melt-waters from the adjoining snow. They also occur along small streams leading from the snow-patch, on wet gravelly areas, and as flushes within

TABLE 1

HIGH MOUNTAIN VEGETATION OF THE AUSTRALIAN ALPS AND SUMMARIZED ENVIRONMENTAL DATA

Alliance	Association Dominants	Structural Form or Subform	Distribution	Habitat
Poa caespitosa–Danthonia nudiflora	*Poa caespitosa* Forst. f. *Danthonia nudiflora* J. Vickery *Calostrophus lateriflorus* F. Muell. *Themeda australis* Stapf.	Sod tussock grassland	Subalpine and alpine	Wide range of high mountain climate; daily temperature fluctuations unusually large during snow-free months owing to cold air drainage into broad valleys. Mainly level and undulating situations. Alpine humus soils, gley podzols, acid marsh soils
Celmisia longifolia–Poa caespitosa	*Celmisia longifolia* Cass. *Poa caespitosa* Forst. f. *Helipterum incanum* D.C. var. *alpinum* F. Muell. *Danthonia frigida* J. Vickery	Tall alpine herbfield	Alpine	Alpine climatic climax. Average annual precipitations 70–120 in., mainly as persistent winter snow. Normal mean monthly temperatures range from maximum of 50–60°F in midsummer to less than 25°F in midwinter. Average annual Meyer ratios 1000–1500. Alpine humus soils, humified peats
Brachycome nivalis–Danthonia alpicola	*Brachycome nivalis* F. Muell. *Danthonia alpicola* J. Vickery *Cardamine hirsuta* L. *Alchemilla novae-hollandiae* Rothm. *Blechnum penna-marina* Kuhn. *Polystichum aculeatum* Schott.	Tall alpine herbfield	Alpine	Rock ledges and precipitous slopes associated with *Celmisia longifolia–Poa caespitosa* alliance
Plantago muelleri–Montia australasica	*Plantago muelleri* Pilger *Montia australasica* Pax. & K. Hoffm. *Caltha introloba* F. Muell. *Brachycome stolonifera* G. L. Davis *Ranunculus inundatus* R.Br. ex D.C. *Oreobolus pumilio* R.Br.	Short alpine herbfield	Alpine	Lower snow patch situations associated with *Celmisia longifolia–Poa caespitosa* alliance. Snow-covered for at least 8 months of the year. Snow-patch meadow soils, poor fen peats

TABLE 1 (*Continued*)

Alliance	Association Dominants	Structural Form or Subform	Distribution	Habitat
Carex gaudichaudiana	*Carex gaudichaudiana* Kunth *Danthonia nudiflora* J. Vickery *Festuca muelleri* J. Vickery *Eleocharis acuta* R.Br. *Poa caespitosa* Forst. f.	Fen	Alpine and subalpine (and at lower levels)	Wide range of alpine and subalpine climates. Level and gently undulating situations; permanently wet and acid, but with a moderate supply of bases. Poor fen peats and acid marsh soils
*Carex gaudichaudiana–Sphagnum cristatum**	*Carex gaudichaudiana* Kunth *Sphagnum cristatum* Hpe.	Valley bog	Subalpine and alpine	As above, but more acid and base-deficient. Soils valley bog peats
Epacris paludosa–Sphagnum cristatum	*Epacris paludosa* R.Br. "*E. serpyllifolia*" Auctt. (non R.Br.) *Callistemon sieberi* D.C. *Richea continentis* B. L. Booth *Restio australis* R.Br. *Carex gaudichaudiana* Kunth *Carpha nivicola* F. Muell. *Astelia alpina* R.Br. var. *novae hollandiae* Skottsb. *Sphagnum cristatum* Hpe.	Raised bog	Subalpine and alpine (and at lower levels)	As above, but slopes steeper, and conditions still more acid and base-deficient. Soils raised bog peats
Epacris petrophila Veronica densifolia	*Epacris petrophila* Hook. f. *Veronica densifolia* F. Muell. *Ewartia nubigena* Beauverd. *Kelleria tasmanica* Domke. *Helipterum incanum* D.C. var. *alpinum* F. Muell.	Fjaeldmark	Alpine	Exposed alpine peaks and plateaux with very strong winds. Lithosols and alpine humus soils
Coprosma pumila–Colobanthus benthamianus	*Coprosma pumila* Hook. f. *Colobanthus benthamianus* Fenzl.	Fjaeldmark	Alpine	Upper alpine snow-patch situations, experiencing severe temperature fluctuations combined with drought during the snow-free months. Lithosols

* Formerly included with *Sphagnum cymbifolium* (sens. lat.)

TABLE 1 (*Continued*)

Alliance	Association Dominants	Structural Form or Subform	Distribution	Habitat
Oxylobium ellipticum–Podocarpus alpinus	*Oxylobium ellipticum* R.Br. *Podocarpus alpinus* R.Br. *Lissanthe montana* R.Br. *Phebalium ovatifolium* F. Muell. *Orites lancifolia* F. Muell. *Prostanthera cuneata* Benth. *Acacia alpina* F. Muell. "*Hovea longifolia*" Auctt. (non R.Br.) *Drimys vickeriana* A. C. Sm. *Leucopogon hookeri* Sond. *Bossiaea foliosa* A. Cunn. *Kunzea peduncularis* F. Muell. *Baeckea gunniana* Schau. *Callistemon sieberi* D.C.	Heath	Alpine and subalpine	Wide range of alpine and subalpine climates, but usually in relatively rocky situations, which become snow-free earlier than the surrounding vegetation. Lithosols, alpine humus soils
Epacris serpyllifolia–Kunzea muelleri	"*Epacris serpyllifolia*" Auctt. (non R.Br.) *Kunzea muelleri* Benth.	Heath	Subalpine and alpine (and at lower levels)	Wide climatic range. Level and gently sloping, acid and poorly aerated situations. Alpine humus soils, gley podzols
Eucalyptus niphophila	*Eucalyptus niphophila* Maiden & Blakely *E. stellulata* Sieb. ex D.C. *E. pauciflora* Sieb. ex Spreng. var.	Subalpine woodland	Subalpine	Subalpine climatic climax. Average annual precipitation 30–80 in., largely as persistent winter snow. Normal mean monthly temperature ranging from maximum of 60–75°F in midsummer to a minimum of 25–30°F in midwinter. Average annual Meyer ratios 400–1000. Alpine humus soils, humified peats

other vegetation. These communities attain their best development again in the Kosciusko area, although they are not uncommon in the Victorian Alps, as on Mt. Bogong, the Bogong High Plains, Mt. Hotham, Mt. Feathertop, Mt. Stirling, Mt. Buller, and on a very small scale on wet gravelly areas on the Baw Baws. Although the same type of carpet-like vegetation is apparently of almost world-wide occurrence in snow-patch areas, the Australian communities are notable for the absence of dwarf woody chamaephytes which are so characteristic of the snow-patch vegetation of the Northern Hemisphere (e.g. the dwarf willows, *Salix herbacea* L., etc.), and appear to be relatively richer in phanerogamic communities than in those dominated by cryptogams.

Tall alpine herbfield vegetation of the *Brachycome nivalis–Danthonia alpicola* alliance is of local occurrence on steep rocky faces, crevices, and ledges of the alpine tract. It occurs in most of the higher areas under discussion, and especially on the steeper mountains, such as Bogong, Hotham, Feathertop, and Buller, on which the chomophyte habitat is well developed. These communities have much in common physiognomically with the rock ledge vegetation of arctic-alpine species in Europe as on Ben Lawers, and on the Black Cuillins on Skye (cf. Poore, undated; Tansley 1939; Pearsall 1950).

The *Celmisia longifolia–Poa caespitosa* tall alpine herbfield alliance is the climatic climax of the alpine tract. The best and most extensive development in Australia is in the Kosciusko area. Here the extensiveness and continuity of the low alpine environment—and hence of tall alpine herbfield which forms the climatic climax—is difficult to match anywhere in Europe, since the mountain areas in Europe, although often larger, are usually steeper and more dissected. The *Celmisia longifolia–Poa caespitosa* alliance is also well developed in Victoria, although less extensively, as on the Spion Kopje–Mt. Nels and other summit areas of the Bogong High Plains; on Mt. Bogong; in the Loch–Hotham–Feathertop area; on Mts. Buller and Stirling; on Mts. Cobberas, Pinnibar, and Gibbo; and on the leeward slopes of Mt. Speculation, the Crosscut Saw, Mt. Howitt, Mt. Magdala, Mt. Lovick, and The Bluff. Another small but interesting occurrence is below the Mt. Cobbler cliffs where relative inaccessibility to livestock has preserved these communities in their near-primitive condition. Most of the Victorian communities are noteworthy for the presence of a broad and silky-leafed *Celmisia* which apparently does not occur in New South Wales or the Australian Capital Territory.

The development of tall alpine herbfield as a climatic climax means that the influence of parent material is relatively slight; indeed, the range of parent materials on which this vegetation occurs on the Australian Alps is very great. This is in strong contrast to the corresponding herbfield vegetation of Europe which develops mainly in association with rocks or ground waters of adequate base status. Under the moist climatic conditions of the British and Scandinavian mountains, furthermore, progressive base depletion and mor formation are thought to be further restricting the already limited distribution of this type of vegetation. In Australia, on the other hand, the herbfield communities appear to be in stable equilibrium owing to the special soil stabilizing processes of base and mineral circulation referred to previously.

Next to suba pine woodland, sod tussock grassland of the *Poa caespitosa-Danthonia nudiflora* alliance is the most abundant and widespread high mountain community on the Australian mainland. It develops mainly in level and undulating situations such as occur along valleys and on broad plateaux, where conditions of cold air drainage or restricted soil aeration or both, commonly prevail. Where cold air drainage is pronounced, as in the headwater region of the Murrumbidgee River, the lower limit of this alliance may be depressed by as much as 1000 ft below the normal subalpine level. Widespread on the Snowy Mountains and Fiery Range, particularly in the Murrumbidgee headwaters, the Kiandra area, Snowy Plains, and Happy Jack's Plain, these communities also occur extensively in Victoria, as on the Bogong High Plains, Dargo High Plains, Howitt Plains, Bryce's Plains, Snowy Plains, Holmes Plain, Bennison Plains, and the Big Plain near Mt. Wellington. An interesting outlier of this alliance—apparently the northernmost of any size—occurs on the Barrington Tops of New South Wales (Fraser and Vickery 1939). It is interesting to record that this alliance descends to lower levels on the north-west of the Monaro Region of New South Wales than in Victoria (where otherwise the vegetation belts are lower in accordance with the more southerly latitude). This is attributed to the stronger development of the high plains type of topography in the Monaro Region to the extent that the resultant cold air drainage effects more than offset the normally higher temperatures of the north.

Poorly aerated but not necessarily wet soils of level to gently sloping situations are characterized by heath vegetation of the "*Epacris serpyllifolia*"–*Kunzea muelleri* alliance. Similar vegetation is also common on many areas of eroded and dried-out bog. These communities are best developed in the Snowy Mountains area and Fiery Range and in parts of the Bogong High Plains, although they are not uncommon in most gently sloping mountain areas. The original character and distribution of these communities have been much modified by grazing and fires.

Heath vegetation of the *Oxylobium ellipticum–Podocarpus alpinus* alliance is common on freely drained, shallow, or rocky soils throughout the Australian Alps. It is best developed in the Kosciusko area where the abundance of exposed rocky surfaces and glacial moraine provide ideal habitat conditions. In the The Bluff–Mt. Howitt–Mt. Cobbler group of mountains, where exposed sandstone habitats predominate, this vegetation is also particularly well developed. Isolated windswept peaks which barely attain subalpine levels (e.g. Mt. Tingiringi) are also frequently dominated by communities of this alliance. The original character and distribution of this vegetation are now difficult to interpret owing to the extensive modification (especially by fire) which has occurred.

Subalpine woodlands of the *Eucalyptus niphophila* alliance are the climatic climax of the subalpine tract and dominate the greater part of the high mountain areas under discussion. The lower strata of these communities vary from grassland to heath depending on whether the soils are relatively deep (the more usual condition) or rocky. The heathy elements have increased greatly on account of frequent fires.

The geographical variation in the level of the tree-line deserves comment. From the northernmost tree-line areas north of Kosciusko to the southernmost in Victoria, the altitude difference is almost 1000 ft. Thus, on Jagungal, north of Mt.

Kosciusko, snow gums are found as high as 6500 ft, on the Kosciusko Plateau at slightly more than 6000 ft, and on Mts. Bogong, Buller, and Stirling at about 5750–5500 ft. Other influences which modify the general pattern are those of local protection or exposure. Thus, on the Perisher Range in the Kosciusko area, the tree-line stands as high as 6500 ft; this is attributable to the protection afforded by the Main Range to the west, and to the general rockiness of the Perisher area, which results in a more rapid melting of snow. Exposed isolated summits or their windward aspects, on the other hand, are commonly bare of trees, like Mt. Cobbler (5342 ft) and Mt. Wellington (5355 ft) in Victoria.

Another interesting latitudinal variation which appears in the southerly subalpine woodlands of the Baw Baw Plateau is the presence of myrtle beech (*Nothofagus cunninghamii* Oerst.), a species which is entirely absent from New South Wales and which elsewhere in southern Victoria occurs only under montane conditions. Its presence in the subalpine tract of the Baw Baws is related to the higher humidities and greater cloudiness; together with an interesting group of Tasmanian species it provides a strong link with conditions in Tasmania.

The ability of a broad-leafed evergreen species (the snow gum) to grow under subalpine conditions of cold and snow cover in Australia is also noteworthy, in view of the dominance of conifers or deciduous trees in most subalpine areas overseas. Thus, *Pinus mugo*, *P. cembra*, and *Larix decidua* form the three-line communities of the more Continental European mountains, whilst *Betula pubescens* Ehrh. often with *Sorbus aucuparia* L. assumes dominance under more oceanic conditions.

Local occurrences of the *Epacris paludosa–Sphagnum cristatum* raised bog alliance are fairly common in acid and base-deficient situations of permanent soligenous wetness in most high mountain areas. Although in their active condition these communities are composed of a regular succession of alternating moss hummocks and hollows associated respectively with acidophilous shrubs and with helophytes and hydrophytes ("regeneration complex"), anthropogenic modification has produced communities which now belong largely to "stillstand" and "degeneration" stages, with relatively little active *Sphagnum*, much eroding peat, and abundant shrubs.

These communities have an interesting distribution in south-east Australia, the northernmost* apparently being on the New England Plateau (Millington 1954) and on the Barrington Tops (Fraser and Vickery 1939). Here the vegetation described appears to be essentially similar to that of the alpine-subalpine mountains further south, although there are certain specific differences.

It is of interest to record the increasing relative importance of bog with increasing humidity and cloudiness, especially in summer, from north to south: for example, there is an estimated 5 per cent. of bog above the winter snow-line on the Bogong High Plains, and about 10 per cent. above the corresponding level on the Baw Baw Plateau. The Dargo High Plains, the Mt. Wellington area, Echo Flat, and other southern high plains areas are similarly rich in bog.

* The *Sphagnum* bogs now recorded from coastal areas of Queensland (Coaldrake, private communication), apparently possess quite different physiognomic dominants, and would be referred to another alliance.

It is also noteworthy that the bogs are generally larger near lower subalpine than at higher levels (e.g. near Mt. Franklin in the Australian Capital Territory and the Bennison Plains in Victoria). This may be due to the longer subalpine growing season, and probably also the fact that the subalpine bogs are older than those in the alps. Prolonged dry spells, rather than high temperatures or low precipitations, appear to be the critical climatic factor.

The *Carex gaudichaudiana–Sphagnum cristatum* alliance occurs as a valley bog in almost level, acid, and base-deficient situations of permanent geogenous or limnogenous wetness such as valleys and upland flats. Its best development is in the Kosciusko area of New South Wales, although smaller occurrences have been observed in Victoria, e.g. on the Baw Baws. This community is essentially transitional between raised bog and acid fen, and in some cases there is evidence of priseral relationship, although elsewhere the valley bog has obviously existed for considerable periods of ecological time. Disturbance of the bog surface, as by fire or grazing, leads to the disappearance of active *Sphagnum*, the drying out and erosion of the surface peat, and invasion by shrubs, resulting in a secondary community, which is often indistinguishable from stillstand or degeneration stages of raised bog.

Poor fen (acid fen) communities of the *Carex gaudichaudiana* alliance occur in wet, level to gently sloping situations such as develop along permanent watercourses, in valleys and on flats where a high water-table is maintained by limnogenous or geogenous influences. Although independent of rock type as such, the development of this vegetation requires the addition of a small amount of base or mineral matter. These rather special physiographic and nutritional requirements probably account for the virtual restriction of considerable occurrences of this alliance to the Snowy Mountains area where the requisite conditions are well developed. However, smaller fens are not uncommon elsewhere in the Australian Alps, as on the Bogong High Plains, the Baw Baws, Mt. Buller, and The Bluff.

Considering the high mountain vegetation of the Australian mainland as a whole, the interaction of climate and parent material is less clearly defined than in the high mountain vegetation of Europe. At the one extreme, the oceanic climate in Britain, expressing itself in the preponderance of acidophilous bog, heath, and grassland, is almost completely dominant. Only in special circumstances is the influence of a basic parent material strong enough to produce a richer herbfield vegetation. In Scandinavia oceanic influences are still strong, but less so than in Britain, with the result that the acidophilous communities, whilst still predominant, are commonly replaced by herbfield and other relatively eutrophic vegetation. Finally, under the drier and (in summer) warmer climatic conditions of the Continent, the influence of parent material becomes even stronger and the proportion of relatively eutrophic vegetation is correspondingly increased.

Although certain broad climatic and primary edaphic effects are also evident from the northernmost to the southernmost high mountain areas of the Australian mainland (e.g. the increased amount of bog, the lower tree-line, and the appearance of myrtle beech) the same relationships do not exist with regard to herbfield vegetation as in Europe. In Australia, the development of herbfield is independent of parent material at least to the extent that it is widespread even on strongly acid

rocks. Nor has evidence yet been obtained, as in Britain and Scandinavia, that progressive base depletion since the Ice Age has been reducing the extent of herbfield plants; on the contrary, base depletion of Australian herbfield soils is apparently minimized through active base and mineral circulation by the vegetation and through earthworm activity. Compared with the high mountain vegetation of Europe, therefore, the Australian vegetation is rich in herbfield communities which further appear to be in equilibrium with present conditions, and in the Kosciusko area of New South Wales the extensiveness of herbfield is still further enhanced by the marked continuity of the alpine plateau which, though glaciated, has not yet been markedly dissected by post-glacial erosion.

Notwithstanding the extensiveness of herbfield vegetation in the alps and of subalpine woodland in the subalps, the Australian high mountain vegetation is also relatively richer in other communities than is the corresponding European vegetation. In the first place, the high mountain flora contains several diverse geographical elements with a wide range of ecological biotypes. There is also a wide range of habitats since, although the main climatic range extends only to low alpine, topographic variations produce middle alpine and even high alpine conditions as mentioned above. Finally, the pedogenic role of the vegetation and of the mountain earthworm offsets the podzolising and mor-forming tendencies which dominate most mountains of similarly high precipitations (Costin 1955*a*) on which a progressively poorer and more uniform vegetation develops.

IV. Community Interrelationships

The interrelationships of the high mountain plant communities have been considered elsewhere (Costin 1954). This information, with certain additional data, can be summarized as follows:

Under alpine conditions of climate, tall alpine herbfield of the *Celmisia longifolia–Poa caespitosa* alliance forms the climatic climax; under subalpine conditions, the climatic climax is formed by subalpine woodland of the *Eucalyptus niphophila* alliance.

Physiographically determined climaxes which replace the alpine climatic climax are the localized tall alpine herbfields of the *Brachycome nivalis–Danthonia alpicola* alliance in crevices, on rock ledges, and on other relatively protected rock faces; the short alpine herbfields of the *Plantago muelleri–Montia australasica* alliance in moist snow-patch environments, on wet gravelly areas, and along associated streams; fjaeldmark of the *Coprosma pumila–Colobanthus benthamianus* alliance in adjacent, relatively dry, and exposed snow-patch situations; and fjaeldmark of the *Epacris petrophila–Veronica densifolia* alliance on the most wind-exposed alpine plateaux and cols.

On imperfectly aerated, though rarely waterlogged, soils in the alpine and subalpine tracts, and under conditions of cold air drainage in the subalpine tract, the alpine and subalpine climatic climaxes are replaced by sod tussock grasslands of the *Poa caespitosa–Danthonia nudiflora* alliance. Although a physiographic climax, these communities, when determined by cold air drainage, often have a very extensive

distribution. Under somewhat drier soil conditions the grasslands grade into heaths of the *Epacris serpyllifolia–Kunzea muelleri* alliance.

In contrast to the above conditions producing sod tussock grassland or *Epacris–Kunzea* heath, relatively rocky and freely drained situations support heaths of the *Oxylobium ellipticum–Podocarpus alpinus* alliance, both in the alpine and subalpine tracts. In the alpine tract, a shorter duration of snow cover, as determined by local physiography, also appears to be important.

In permanently wet situations under conditions of increasing acidity and base-deficiency the above communities are replaced respectively by fen (*Carex gaudichaudiana* alliance), valley bog (*Carex gaudichaudiana–Sphagnum cristatum* alliance), and raised box (*Epacris paludosa–Sphagnum cristatum*), developing as physiographic climaxes.

In most parts of the Australian Alps the relationships indicated above, and the relationships within the alliances themselves, have been much modified by land use, largely the summer grazing of sheep and cattle, associated with recurrent fires, and more recently by engineering and tourist operations. The nature of this modification will be mentioned in a forthcoming paper.

V. Ecological Types of High Mountain Areas

In this overall treatment the high mountains of the Australian mainland, as depicted in Figure 1, can be considered as belonging to one or more of the following five broad ecological types:

Alpine-subalpine plateau mountains
Steep alpine-subalpine mountains
Subalpine plateau mountains
Steep subalpine mountains
Montane plateau mountains.

(*a*) *Alpine-Subalpine Plateau Mountains*

This type of mountain (Plate 1, Fig. 1), comprising the Kosciusko area in New South Wales and the Bogong High Plains in Victoria, includes the greatest altitudinal and physiographic range of environments. It is consequently richest in plant communities: subalpine woodland, the alpine herbfields, sod tussock grassland, and the heaths and bogs are all well represented; at Kosciusko the fjaeldmark and fen alliances are also present although they are virtually lacking on the less elevated Bogong High Plains.

(*b*) *Steep Alpine-Subalpine Mountains*

This type of mountain (Plate 1, Fig. 2) is found in a large number of relatively isolated areas in the Victorian Alps, namely, Mt. Bogong, the Mt. Loch–Mt. Hotham–Mt. Feathertop area, Mt. Buller, Mt. Stirling, and the long arc of mountains commencing at Mt. Cobbler and continuing through Mt. Speculation and the Crosscut

Saw to Mts. Howitt and Magdala, No. 1 and No. 2 Divides, Mt. Lovick, and The Bluff.

Because of their relative steepness and consequent dryness, and the fact that they happen to be somewhat lower than the alpine-subalpine plateau mountains, the mountains of this type are not well supplied with bogs and fens and the grassland and heath communities of gentler sloping situations. They are relatively lacking in the exclusively alpine communities other than the tall alpine herbfields. In other words, the vegetation consists largely of subalpine woodland, tall alpine herbfields, and *Oxylobium–Podocarpus* heath; it contains only small occurrences of short alpine herbfield, sod tussock grassland, *Epacris–Kunzea* heath and bogs, and is virtually lacking in fjaeldmark and fen.

(c) *Subalpine Plateau Mountains*

The mountains of this group (Plate 2, Fig. 1) resemble those of the first type in their extensiveness and consequent development of communities of wet and gentler-sloping terrain, but they are lacking in alpine vegetation. Subalpine woodland, sod tussock grassland, bog, and *Epacris–Kunzea* heath are therefore well represented; occasionally there is also *Oxylobium–Podocarpus* heath and fen, but the alpine herbfield and fjaeldmark communities are absent. Most of the Australian high mountain country belongs to this type: the greater part of the higher catchments (other than the Kosciusko area) of the Snowy, Murray, Tumut, and Murrumbidgee Rivers in New South Wales; and the Buffalo Plateau, the Baw Baw Plateau, Echo Flat, the Dargo High Plains, Howitt Plains, Conglomerate Water, Bryce's Plains, Snowy Plains, the head of Bennison Creek, Bennison Plains, Holmes Plain, Mt. Wellington, and similar areas in Victoria.

(d) *Steep Subalpine Mountains*

The lack of elevated areas and of gentler slopes in this group of mountains (Plate 2, Fig. 2) limits the vegetation largely to subalpine woodland and *Oxylobium–Podocarpus* heath, with occasional smaller occurrences of sod tussock grassland and bog. The high mountains of the Australian Capital Territory and their environs, and such isolated subalpine peaks as The Viking and The Razor: Mts. Cobberas*, Gibbo*, and Pinnibar*; and Mts. Clear, Skene, and Shillinglaw belong to this group.

(e) *Montane Plateau Mountains*

Although no truly high mountain country occurs further northwards than the Australian Capital Territory, special physiographic conditions on the Barrington Tops and New England Plateau have favoured the persistence of fragments of high mountain vegetation which admit these areas to the present discussion. Thus, on the Barrington Tops, bog and sod tussock grassland develop on the wet upland flats and adjacent lower slopes (Fraser and Vickery 1939), whilst wet areas on the New England tableland support bog (Millington 1954).

* These mountains, with their small development of alpine herbfields as physiographic climaxes, almost qualify as "steep alpine-subalpine".

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EXPLANATION OF PLATES 1 AND 2

PLATE 1

Fig. 1.—Alpine subalpine plateau mountain: Mt. Lee and Carruthers Peak, as seen across the Upper Snowy River from near the tree-line at Kosciusko.

Fig. 2.—Steep alpine-subalpine mountain: Mt. Feathertop and the Razorback, as seen from Mt. Hotham. The edge of the Bogong High Plains, in the alpine–subalpine plateau mountain group, is seen in the right background.

PLATE 2

Fig. 1.—Subalpine plateau mountain: the headwaters of the Moroka River, as seen from Mt. Wellington. The Bluff–Mt. Howitt–Mt. Cobbler arc of mountains, in the steep alpine-subalpine mountains group, is seen in the background, partly obscured by cloud.

Fig. 2.—Steep subalpine mountains: The Viking and the Razor (background) with the Devil's Staircase (right middle distance), as seen across the Wonnangatta Valley from near Mt. Howitt.

NATURE AND DISTRIBUTION OF RAIN-FORESTS IN NEW SOUTH WALES*

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Summary

Rain-forest has a discontinuous distribution along the coast and adjoining ranges of New South Wales, extending to altitudes of over 4000 ft. Four major subformations can be recognized, along with two other structural forms which may deserve subformation status. The subformations have been defined as tropical, subtropical, temperate, and dry rain-forest. Six floristic alliances and their associations are briefly described.

For the widespread development of rain-forest an annual rainfall exceeding 60 in. is required, though rain-forest is found under much lower rainfalls in places favoured by the soil or topography. The *Hemicyclia* alliance (dry rain-forest) is found in areas showing a distinctly seasonal rainfall distribution, while the *Nothofagus* alliance (temperate rain-forest) requires cold and very moist conditions. The *Castanospermum* alliance occurs along creek banks, usually away from the main rain-forest patches, and the *Cupaniopsis* alliance is found close to the coast, apparently requiring wind-borne supplies of moisture and mineral nutrients for its development. The *Argyrodendron* (tropical) and *Ceratopetalum* (subtropical) alliances occur under similar climatic conditions in the north, but with the *Ceratopetalum* alliance restricted by competition to the less fertile soils. In the south of the State, where climatic sifting has removed many tropical rain-forest species, the *Ceratopetalum* alliance occurs on the richer soils.

The discontinuity of the rain-forest distribution has been brought about by past climatic changes. Human influence has always restricted rain-forest spread, and since European settlement the area of rain-forest in New South Wales has been reduced by about half.

I. Introduction

The aim of the present paper is, firstly, to describe the structure and composition of the rain-forest communities in New South Wales, and, secondly, to discover those factors which are of the greatest importance in determining the nature and distribution of rain-forest.

Particular emphasis has been placed on the rain-forests north of the Bellinger River, since these not only include all the main forms of rain-forest encountered in New South Wales, but also represent the bulk of the State's commercial rain-forest areas from a forestry viewpoint.

The present paper is based largely on data collected during two field trips to the Casino and Coff's Harbour forestry districts, followed by the analysis of collected plant and soil materials at the laboratories of the Department of Botany, University of Sydney.

*The present paper is an abridged and slightly modified version of an honours thesis (Baur 1954) presented to the University of Sydney in December 1954.

†Forestry Commission of New South Wales, Coff's Harbour, N.S.W.

The communities studied were all characterized by a more or less closed canopy of one or usually more layers of mesomorphic trees and shrubs, generally from a number of different genera and families. Lianes and epiphytes were commonly abundant, but *Eucalyptus* spp., except as a fairly obvious remnant from an earlier community, were absent. A more detailed definition of rain-forest and its various subformations will be considered later in this review.

II. Distribution of Rain-forest in New South Wales

General discussions on the extent of rain-forest in New South Wales have been given by the Forestry Commission of New South Wales (1947), Wood (1950), and Francis (1951), and maps have been included by the last two authors. All three references contain inaccuracies and omissions. The Forestry Commission publication fails to mention or to show on its map the rather extensive stands on rain-forest in the Barrington Tops area, but otherwise gives the most complete account of rain-forest distribution and the most accurate map. Francis makes no mention of the important rain-forests of the Hastings River watershed, whilst Wood, in a very small scale map, gives these communities undue prominence but barely acknowledges the presence of the equally important Dorrigo Plateau rain-forests.

The area of rain-forest in New South Wales has been estimated as about 700,000 acres, of which some 450,000 acres have been dedicated as state forest. (Forestry Commission of N.S.W. 1947). In addition large areas formerly occupied by rain-forests have been cleared to make way for farming land.

Data on the distribution of rain-forest are still far from complete, though the major areas are now fairly well known. The map (Fig. 1) shows the presence of five main areas in New South Wales. Besides these there are numerous smaller and relatively isolated patches, and extensive areas in which rain-forest occurs along the banks of creeks and in sheltered gullies. The five major areas are:

The McPherson Range and Richmond–Tweed Valleys.

The Dorrigo Plateau and Bellinger River headwaters.

The Hastings River headwaters, with extensions north to the Carrai Plateau, and south to the Bulga and Comboyne Plateaux.

The Barrington Tops district.

The Illawarra district and Robertson highlands.

The Illawarra rain-forest has been almost entirely destroyed by clearing, as have considerable portions of the Richmond–Tweed rain-forest (the "Big Scrub" of the early settlers) and the Dorrigo and Bulga–Comboyne rain-forests. Similarly the alluvial flats of all the major coastal streams north of the Shoalhaven River originally supported dense rain-forests which have been destroyed, first for their timber wealth (particularly the red cedar, *Cedrela toona* var. *australis*), and later to make way for agriculture.

The rain-forest areas shown enclosed by the broken line in Figure 1 are of particular importance and have been reserved for more detailed discussion in Section III. Short descriptions of all the areas are given in Sections II(a) to II(d) below.

Fig. 1.—Rain-forest distribution in New South Wales

(a) *Rain-forest North of the Clarence River*

The far northern areas will be dealt with more fully in the next section. The few remaining pockets of rain-forest along the Richmond–Tweed lowlands are characterized by their general luxuriance. Francis (1951) has compared these stands, remnants of the Big Scrub, with the truly tropical rain-forests of North Queensland. The species present here are very mixed and dominants are hard to recognize. *Ficus* spp. and *Argyrodendron* spp. are relatively common, and apparently *Cedrela toona* and *Flindersia* spp. were originally frequent. A number of important Queensland species reach their southern limit here. This type of rain-forest is confined to areas of basalt or alluvium under high rainfall conditions.

Similar soils further from the coast support an almost equally luxuriant community, in which the *Argyrodendron* spp. are rather clearly dominant, while at higher altitudes *Dysoxylum fraseranum* competes with the argyrodendrons as the dominant species. Still higher, on the frequently clouded points of the McPherson Ranges small stands of *Nothofagus moorei* occur. High rainfall areas with less fertile soils support a rain-forest dominated by *Ceratopetalum apetalum* (coachwood) or, in more adverse sites, wet sclerophyll forest.

Where rainfall decreases, particularly in the river valleys, rain-forest is usually absent except as a fringing community along the watercourses. The vegetation in these areas (e.g. the Richmond valley north and west of Kyogle) is typically a tall woodland *Eucalyptus* association, with a narrow fringing rain-forest containing a high proportion of *Castanospermum australe*, *Grevillea robusta*, and *Podocarpus elatus*. Away from the creeks, but in locally favoured situations, patches of a low growth of rain-forest species forming a closed canopy are commonly encountered. These contain numerous species of the Sapindaceae and Euphorbiaceae, and are frequently overtopped by an open stand of hoop pine, *Araucaria cunninghamii*. Such areas are locally known as "dry scrub", "viney scrub", or "bastard scrub", "scrub" being a general North Coast term for rain-forest.

Most of the Clarence valley is an area of poor soils and low rainfall. Rain-forest, now completely cleared, once extended along the Clarence River banks to slightly west of Grafton, while small dry scrub pockets and fringing rain-forest occur in parts of the western valley. To the south drainage is off the Dorrigo Plateau, the second major stand of rain-forest in this State.

(b) *Rain-forest on the Dorrigo Plateau*

The Dorrigo Plateau has an elevation of about 1500 ft in the east, where it rises up sharply from the coast behind Coff's Harbour, and then rises gently to more than 5000 ft in the west (Point Lookout, 5250 ft). It decreases gradually in elevation to the north but drops steeply down to the Bellinger River in the south. Extensions of the Plateau occur in rugged highland to the south of the Bellinger valley. The eastern part of the plateau is of shale, but in the west this has been covered by basalt flows of Tertiary age. The town of Dorrigo lies on the junction of the shale and basalt. The shale region is still largely forested and contains mainly a *Ceratopetalum*-type rain-forest. *Nothofagus* occurs, but only as an associate species to

Ceratopetalum along watercourses. Wet sclerophyll forest, containing *Eucalyptus microcorys*, *E. saligna*, *E. companulata*, and *E. pilularis*,* is found along the ridges.

The basalt region has been almost entirely cleared for dairying pursuits. Only isolated outliers of basalt are still forested, supporting an *Argyrodendron* rain-forest. Associated with these basalt pockets are a number of small natural grasslands on the basalt, surrounded by rain-forest. The main basalt region near Dorrigo originally contained a rain-forest with much *Dysoxylum fraseranum*, *Cedrela*, *Geissois benthami*, *Gmelina leichhardtii*, and other commercially valuable species. *Nothofagus* occurred on rocky knolls near the southern scarp of the Plateau, where the land is frequently covered in mist. At higher elevations further west, rain-forest is absent from the basalt plateau and its place is taken in part by a community of snow grass (*Poa* spp.), and scattered snow gums (*E. pauciflora*). Valleys cutting through this plateau are fringed by a *Nothofagus* rain-forest, containing also some *Ceratopetalum* and *Orites excelsa*.

Rain-forest continues round the Bellinger and Nambucca River watersheds, but is absent from most of the northern Macleay valley. Areas of *Ceratopetalum* and *Nothofagus* rain-forests occur further west in the Styx River region. The coastal lowlands support mainly wet sclerophyll forest, but with rain-forest communities of varying complexity occupying most gullies. These gully rain-forests are a characteristic feature of the coastal vegetation from north of Coff's Harbour to south of Sydney.

(c) *Rain-forest between the Macleay and Hunter Rivers*

West of Kempsey is the Carrai Plateau, containing both *Ceratopetalum* rain-forests and more complex communities with much *Cedrela*. These are linked to the large Hastings watershed rain-forest by patches of gully rain-forest. The Hastings rain-forest is predominantly of *Ceratopetalum*, particularly in the west where some ecological studies have been made by Burges and Johnston (1953). More complex communities dominated by *Dysoxylum* or *Argyrodendron* are present on areas of better soil, whilst at high elevations in the north of the region (Mt. Banda Banda, 4140 ft) are extensive areas of *Nothofagus* rain-forest. In the south the rain-forest extends on to the Bulga and Comboyne Plateaux, large areas of which have been cleared for agriculture. The Manning River originally supported rain-forest along its lower banks and small pockets occur in the western valley. Some of these follow creeks up into the Barrington Tops rain-forest area. This region has been extensively studied by Fraser and Vickery (1937, 1938, 1939). The parent rock is basalt and the area has a high rainfall. Higher elevations support a *Nothofagus* rain-forest, though the plateau top itself carries mainly a snow grass community with some snow gum. At lower elevations is a fairly luxuriant mixed rain-forest community, in which *Schizomeria ovata*, *Ackama muelleri*, *Doryphora sassafras*, and *Cryptocarya glaucescens* are common. No *Ceratopetalum* or *Argyrodendron* spp. are found in this area.

Small patches of rain-forest occur between Barrington and the coast, though the dominant vegetation is sclerophyll forest. Isolated pockets near the coast have been

*The terminology of *Eucalyptus* species throughout the present paper is that of Blakely (1955).

described by Osborn and Robertson (1939), while the species from the Krambach district have been recorded by Maiden (1895). West of the Barrington Tops, rain-forest occurs on a number of the higher outlying mountains, and is found also in sheltered sites at lower elevations. Several such areas occur in the Liverpool Range foothills west of Murrurundi.

(d) *Rain-forest in Southern New South Wales*

South of the Hunter River, which originally carried rain-forest along its lower reaches, some fairly rich communities are found in gullies in the Gosford-Wyong district. The extensive Hawkesbury Sandstone area, however, contains only occasional patches of depauperate rain-forest in some of its gullies. Basalt-capped peaks in the Blue Mountains and also further north (Nullo Mountain, and Mt. Coricudgy near Rylstone) support a *Ceratopetalum* rain-forest, as do the deeper, sheltered gullies of this region. Such sites at Mt. Wilson have been studied by Brough, McLuckie, and Petrie (1924) and by McLuckie and Petrie (1926).

South of Sydney rain-forest occurs with some luxuriance in gullies overlying Narrabeen chocolate shales, and originally covered most of the Illawarra Plain from Bulli to the Shoalhaven River. This area has now been almost completely cleared, though remnants along the western scarp still exist. Some of these were studied by Davis (1936, 1941) and were shown to contain a mixture of species from the *Ceratopetalum* type and from the more complex northern communities. Rain-forest extends up to the eastern edge of the Robertson Plateau on the basalt and, under high rainfall conditions, also occurs on the adjacent Wianamatta Shale where the dominant species are *Doryphora sassafras* and *Acacia melanoxylon* (Phillips 1947).

South of the Shoalhaven River no extensive areas of rain-forest occur. Only a few of the typically northern species survive far south of the Shoalhaven, and there is an increasing proportion of Victorian temperate species entering into the sheltered gorges. The transition to the myrtle beech (*Nothofagus cunninghamii*) rain-forests of southern Victoria and Tasmania takes place gradually along this length of coast and in eastern Victoria. Myrtle beech itself does not occur in New South Wales but is found in the ranges of eastern Gippsland (Forests Commission of Victoria 1948).

III. Rain-forest Localities in Northern New South Wales

(a) *Geology*

The country between the Bellinger River and the Queensland border (Fig. 2) is characterized by two elevated areas, the Dorrigo Plateau at the south and the McPherson Ranges in the north. Between these lies the extensive Jurassic sedimentary basis (Clarence series) of shales, sandstones, conglomerates, and coal measures. The Dorrigo Plateau is an elevated area of shales, probably Silurian, which have been covered from the west by a Tertiary basalt flow.

Stretching north from the Dorrigo Plateau is a long spur known as the Coast Range. This extends from Coff's Harbour to the mouth of the Clarence River, running parallel to the coast and roughly 5 miles inland. Its average height is about 1000 ft, but it rises in places to 2500 ft. In the south it is composed of the Silurian shales and in the north of rocks from the Clarence series.

The McPherson Ranges and their spurs are mainly formed from a succession of Tertiary larva flows which cover the Clarence series. These flows also cover much of the lower Richmond Valley, reaching the coast between Ballina and Point Danger. The flows contain both basic and acid rocks, and in places the complete series can be seen, with upper and lower basalt flows sandwiching a series of acid rocks including rhyolite, obsidian, and trachyte. Small areas of basalt are found to the south and west of the main flows, mainly along the low ridge that forms much of the Richmond Range.

(*b*) *Climate*

Typical rainfall figures are shown in Table 1. The general picture is one of high rainfall along the ranges and closely adjacent lowlands, with an extensive low rainfall area occupying most of the Clarence Basin.

TABLE 1

MEAN ANNUAL RAINFALL—NORTH COAST LOCALITIES

Station	Years of Record	Rainfall (in.)	Station	Years of Record	Rainfall (in.)
Brooklana	32	65	Grafton	72	36
Byron Bay	52	75	Kyogle	31	45
Casino	71	43	Mt. Pikapene State Forest	17	42
Clouds Creek	15	51	Newfoundland State Forest	7	45
Coff's Harbour	36	64	Roseberry Nursery	14	45
Dorrigo	28	74	Whian Whian State Forest	10	90

In the upper valley of the Richmond River rainfall is also low, though there is evidence that the forested ranges receive higher falls than the nearby valley bottoms, where most weather stations are situated. Thus Munns (1953) states that Roseberry, 13 miles upstream from Kyogle and with an elevation of about 400 ft, has a corrected rainfall of 38 in., while Toonumbar State Forest, 3 miles away but with an altitude of 1200 ft, receives 56 in.

Throughout the region there is a tendency for wet summers, preceded by dry winters and springs. This is clearly shown by the monthly averages for Mt. Pikapene State Forest (Table 2).

Temperatures along the coastal section of the region are warm in summer and mild in winter with occasional frosts. Away from the coast frosts are frequent in the winter and on rare occasions snow has been recorded at stations higher than about 2500 ft. Table 3 gives mean monthly temperatures for two localities, one coastal and the other on the Dorrigo Plateau.

(*c*) *Vegetation North of the Clarence River*

The luxuriant *Argyrodendron*-dominated rain-forests are common in the McPherson Ranges. Good examples can be seen on the Queensland side of the

border near Binna Burra Lodge, Lamington National Park; at Wiangarie State Forest, 14 miles north of Kyogle; at Whian Whian State Forest, 16 miles north of Lismore; and on Mt. Lindsay, on the Queensland border at the head of the Richmond River. At Tooloom Plateau and Acacia Plateau, both about 12 miles westwards from Woodenbong, similar communities occur, but with a tendency for dominance by *Dysoxylon fraseranum*.

TABLE 2

MONTHLY RAINFALL AVERAGES—MT. PIKAPENE STATE FOREST

17 years to 1953

Month	Rainfall (in.)	Month	Rainfall (in.)	Month	Rainfall (in.)
Jan.	6·32	May	1·96	Sept.	1·38
Feb.	6·05	June	4·09	Oct.	2·95
Mar.	6·32	July	1·69	Nov.	3·70
Apr.	1·93	Aug.	1·31	Dec.	4·27

At Lamington National Park, acid volcanic rocks close by the *Argyrodendron* rain-forests support typical *Ceratopetalum* communities, with *Eucalyptus campanulata* wet sclerophyll forest in the more exposed parts. More elevated points carry stands

TABLE 3

MEAN MONTHLY TEMPERATURES

Month	Clouds Creek (1950 ft)		Newfoundland S.F. (250 ft)	
	Mean Max.	Mean Min.	Mean Max.	Mean Min.
Jan.	79·9	57·9	84·1	66·4
Feb.	77·9	57·1	82·1	66·3
Mar.	75·3	52·7	80·2	63·9
Apr.	70·6	43·3	76·0	56·2
May	66·5	37·5	72·8	51·2
June	60·9	33·4	68·3	47·7
July	60·6	31·5	65·5	45·1
Aug.	64·0	32·8	68·2	46·6
Sept.	69·0	37·5	73·6	50·6
Oct.	72·3	44·1	75·9	55·4
Nov.	77·7	51·0	80·2	61·5
Dec.	79·0	54·9	81·9	64·4

of *Nothofagus*. One small area, which according to Herbert (1951) occurs on volcanic glass, carries a stand of mallee (*Eucalyptus codonocarpa*); the pocket is fringed by a poor *Ceratopetalum* rain-forest.

Fig. 2.—North-eastern New South Wales. *S.F.*, State Forest; *N.P.*, National Park

At Whian Whian the complete range of volcanic rocks is present, and upper and lower *Argyrodendron* communites are separated by a belt of *Ceratopetalum* rain-forest and *Eucalyptus pilularis–E. saligna* wet sclerophyll forest on the acid rocks. The lower-altitude *Argyrodendron* rain-forest appears to be the largest Big Scrub remnant still existing; unfortunately it has been rather heavily logged.

Gullies through these *Argyrodendron* stands are bordered by a somewhat different community, in which *Elaeocarpus grandis* is dominant.

The vegetation of Mt. Lindsay shows a transition from the relatively dry valley of the Richmond River (altitude about 500 ft) to the frequently cloud-bound heights of the peak (altitude about 3800 ft, but with sheer cliffs above 3000 ft). The valley bottom runs through Jurassic shales but soils from the base of the cliffs down to the river all show signs of basalt influence. In the valley vegetation is a tall woodland of *Eucalyptus hemiphloia* and *E. tereticornis* associated with *E. melliodora* and *E. decepta*, giving way higher up the slope to a wet sclerophyll forest of *E. saligna*, *E. microcorys*, and *E. wilkinsoniana*. At about 1800 ft the forest is reduced to an open stand of veteran *E. saligna* and *Casuarina torulosa*, and slightly higher is the edge of the rain-forest, with a fringing tangle of vines, including much *Lantana*. Lower levels of the rain-forest are dominated by *Argyrodendron*, and elements from this community persist to near the base of the cliffs. Forming a thin belt around the cliff-base is a low (30–40 ft) stand of *Schizomeria ovata* and *Banksia integrifolia*, with a shrubby understorey. On steep slopes at slightly lower levels are denser, more mixed stands of similar low height, with their branches festooned by a pendent moss. An overstorey of *Araucaria cunninghamii*, also moss covered, is present, and epiphytic ferns are very common, even coating rock slopes.

The river-bank rain-forests which fringe the watercourses in the drier areas were examined at Moore Park, a small flora reserve 3 miles upstream from Roseberry Nursery; at Mt. Pikapene State Forest, about 25 miles south-west of Casino; and along Myrtle Creek, between Casino and Grafton. In the first two localities the communities are fairly rich in species, and are dominated by *Castanospermum australe*, *Grevillea robusta*, and *Podocarpus elatus*. At Myrtle Creek the stand is very impoverished, and has *Eugenia ventenatii* as its dominant species.

Dry scrubs are also common in these areas. The main area is at Mt. Pikapene State Forest where an extensive stand occurs on basalt along the eastern fall of the Richmond Range. Over 1000 acres have been converted to *Araucaria* plantation since 1939. Surrounding the dry scrub is a tall woodland of *Eucalyptus maculata* and *E. rummeryi*. Similar communities are found at Unumgar State Forest, on the southern side of Richmond River opposite Mt. Lindsay; in the upper Clarence valley near Koreelah; and in the Upper Tweed valley at Mebbin State Forest. The Koreelah stand is very small, occupying a single steep slope adjacent to the Lindsay Highway. The overstorey of *Araucaria* is missing here, and the ground surface is extremely stony.

(*d*) *Vegetation South of the Clarence River*

Most of the Clarence basin carries tall woodland, predominantly of *Eucalyptus maculata*, while the northern section of the Coast Range, with very poor soils derived

from the Jurassic sandstones and conglomerates, supports a dry sclerophyll forest of *E. planchoniana* and *E. micrantha*. The junction with the Silurian shales occurs in the Barcoongere and Newfoundland State Forests, about 10 miles north of Woolgoolga. Better soils in this region carry *E. pilularis*, but rain-forest is absent. The land here is being used for the planting of the American slash pine (*Pinus elliottii*, syn. *P. caribaea*) and it appears that while the *E. pilularis* sites will produce good stands of *Pinus*, the *E. planchoniana* sites are worse than marginal.

The southern end of the Coast Range carries chiefly a wet sclerophyll forest dominated by *E. pilularis*, with a rain-forest intermediate in character between the *Argyrodendron* and *Ceratopetalum* types in the gullies. These rain-forests are frequently overtopped by veteran stems of *Eucalyptus grandis*. Similar vegetation is found along the coast south of Coff's Harbour and up into the eastern foothills of the Dorrigo Plateau. Good examples of the gully rain-forests occur at Bruxner Park, a flora reserve on the Coast Range near Coff's Harbour, and at Pine Creek State Forest, on the Pacific Highway between Coff's Harbour and Urunga. Present forest policy in such gullies aims at converting the rain-forest, which is largely unmerchantable, to stands of *E. grandis*.

A type of rain-forest community, frequently dominated by windswept trees of *Tristania conferta* and *Cupaniopsis anacardioides*, occurs commonly as a very narrow band just back from the sea along many of the headlands near Coff's Harbour. An excellent example is seen about 2 miles north of the town. The destruction of this community frequently leads to the death of more economically valuable trees immediately inland, possibly due to the unimpeded entrance of salt-laden wind and spray from the sea. Another unusual rain-forest community, rather sparsely canopied but containing typical rain-forest species, borders a creek flowing through Recent beach sand deposits at Pine Creek State Forest. This stand contains much *Cupaniopsis anacardioides*, with *Archontophoenix cunninghamii* along the creek bank.

The eastern part of the Dorrigo Plateau, with underlying shale, carries mainly a *Ceratopetalum*-dominated rain-forest, with wet sclerophyll forest along the ridges. Excellent examples occur at Orara West State Forest and Brooklana, both about 10 miles east of Dorrigo township; at Dome Mountain, about 5 miles south-east of the town; and at Moonpar State Forest, about 10 miles north-west. Much of this rain-forest country originally carried also an overstorey of *Araucaria*, which has since been removed. At Brooklana attempts were made during 1938-42 to clear the rain-forest and establish *Araucaria* plantations. However, spring frosts caused the death of the young trees on all but the highest topographic positions, and the area has since been replanted with *Pinus taeda* and *P. elliottii* which are growing well. Creek sides at Brooklana and Dome Mountain support a fringe of *Nothofagus*, though the *Nothofagus*-dominated communities themselves are only found on the higher elevations west of Dorrigo. Altitude at both Dome Mountain and Brooklana is between 1700 and 2000 ft.

Throughout this area, as well as in the more northern rain-forest zone, there are clear signs of the sclerophyll forest being invaded by the rain-forest. Fine examples can be seen at Moonpar, where the original community was of *Eucalyptus microcorys* and *E. saligna*, and at Orara West, with the overstorey of *Tristania*

conferta and *Callitris macleayana*. At the latter site the *Tristania* has produced an A_0 litter layer up to 6 in. deep.

Clouds Creek is situated beyond the main rain-forest area, about 16 miles north of Dorrigo, on the road to Grafton. Most of the forest is of *E. microcorys* and *E. saligna*, while sheltered gullies support a *Ceratopetalum* rain-forest. In several places the shale has been covered by basalt, outliers of the main western Dorrigo flow, and these support an *Argyrodendron* rain-forest. Within this basalt area are a number of small clearings covered by dense grass growth, with a very narrow fringe of *E. saligna* and the rain-forest margin immediately behind. *Pinus taeda* planted on one of these "plains" has shown phenomenal growth. The rain-forest surrounding the plains contains scattered *E. saligna*, suggesting a gradual encroachment on to the grassland, with an intermediate eucalypt stage.

IV. Rain-forest Structure

Structure has been described (Beadle and Costin 1952) as the spatial arrangement of plants within a community. Richards (1952) has discussed this very fully, in relation to the tropical rain-forest, and his remarks apply generally to the rain-forest communities of New South Wales.

Under local conditions, rain-forests can be recognized in the field more readily than the features which distinguish them from other formations can be defined. Neither Schimper's (1935) "evergreen, hygrophilous forest" nor Beadle's and Costin's "closed community dominated by usually mesomorphic meso- or megaphanerophytes forming a deep, densely interlacing canopy in which lianes and epiphytes are invariably present, with mesomorphic subordinate strata of smaller trees, shrubs and ferns and herbs" are truly satisfactory in that both definitions exclude communities that are characteristically regarded as being rain-forest. Nonetheless these communities do share to a greater or less extent a number of distinctive structural features, which themselves are capable of considerable variations in importance from one community to another.

Following Richards (1952, p. 20) these features are:

(i) The stratification and nature of the trees, shrubs, and herbs.

(ii) The presence and nature of (1) lianes, (2) stranglers, and (3) epiphytes.

Stratification is invariably present in New South Wales rain-forests and the individual storeys are usually well defined, though in certain sites, notably on steep slopes and in immature stands, a degree of merging occurs. Excluding herb layers, up to five different storeys can be recognized, whilst a sclerophyllous overstorey may also sometimes be present. Herbs are usually rare except where the overhead canopy is locally sparse. The trees are typically evergreen, but deciduous or partly deciduous species are present in some stands, usually in the upper storeys; such species include *Brachychiton* spp., *Erythrina vespertilio*, *Flindersia australis*, *Cedrela toona*, and *Melia dubia*.

Buttressing is particularly common in some communities, and imparts a most characteristic appearance to the whole stand. Cauliflory is very rare in New South Wales rain-forests; only *Hedraianthera porphyropetala* (family Celastraceae) shows

TABLE 4

SUMMARY OF STRUCTURAL CHARACTERISTICS—NORTH COAST RAIN-FOREST SITES

a, absent; r, rare; p, present; +, common; ++, very common

Locality	Type of Rain-forest	Tree Layers (> 20 ft) Present	Overstorey*	Buttressing	Lianes	Vascular Epiphytes	Remarks
Mt. Lindsay	*Argyrodendron*	3		++	p	++	
Wiangarie State Forest	*Argyrodendron*	3		++	+	++	
Whian Whian	*Argyrodendron*	3		++	+	p	Upper basalt flow
Whian Whian	*Argyrodendron*	3		++	+	+	Lower basalt flow
Clouds Creek	*Argyrodendron*	2	p	++	+	p	Adjoining grassland
Tooloom Plateau	*Dysoxylum*	3		++	p	p	
Whian Whian	*Ceratopetalum*	2	p	p	p	p	
Brooklana	*Ceratopetalum*	2	p	a	r	a	
Orara West	*Ceratopetalum*	2	p	r	r	r	Under *Tristania*
Orara West	*Ceratopetalum*	2		r	p	p	
Clouds Creek	*Ceratopetalum*	2		r	r	r	
Moonpar State Forest	*Ceratopetalum*	2	p	r	r	a	Under *E. microcorys*
Moonpar State Forest	*Ceratopetalum*	2		r	p	r	
Dome Mountain	*Ceratopetalum*	3		p	p	p	Top storey of *Araucaria*
Unumgar State Forest	Dry scrub	2		r	++	+	
Koreelah	Dry scrub	2		r	++	p	
Mt. Pikapene State Forest	Dry scrub	2		r	++	r	
Mt. Lindsay	*Schizomeria–Banksia*	1		a	a	r	Community at cliff base
Coff's Harbour	Headland	1		r	+	a	On windswept headland
Moore Park	*Castanospermum*	2		p	p	r	
Wiangarie State Forest	*Elaeocarpus grandis*	3		+	++	+	Storeys tending to merge
Bruxner Park	*Sloanea woollsii*	2	p	+	p	p	

*Overstorey refers to typically sclerophyllous species, remnants of an earlier community.

it clearly, though *Castanospermum* and *Dysoxylum fraseranum* possess it to a lesser extent.

Lianes are present in most communities, and may be very frequent. Two main types occur, one tall-growing and usually possessing thick, rope-like stems, and the other low and rather wiry. Stranglers are present in many communities but are seldom very common. In New South Wales they are all species of *Ficus*, with one insignificant exception (*Quintinia sieberi* on tree ferns).

Epiphytes are a distinctive feature of most rain-forest communities. Non-vascular epiphytes are invariably present, at least on the lower trunks of the trees, and in some communities (e.g. parts of Mt. Lindsay) dominate the whole appearance of the stand. Vascular epiphytes, probably always either orchids or pteridophytes, are also frequently present and may be very common.

Table 4 summarizes some of the more important features of rain-forest structure in various localities in northern New South Wales. One important group of rain-forests is not included here although it occurs fairly commonly in New South Wales. This is the rain-forest dominated by *Nothofagus moorei*, which has been thoroughly studied by Fraser and Vickery (1938) at Barrington. Its structure is similar to the stands dominated by *Ceratopetalum apetalum*, but with a denser crowned upper storey and with buttressing and lianes rare. Vascular epiphytes in the form of the beech orchid (*Dendrobium falcorostrum*) are sometimes very common. Quite frequently the second tree layer is very scattered, so that only one tree layer can be recognized.

Excluding the *Nothofagus* stands, Table 4 shows the presence of three well-defined subformations in the area, plus several others which are more local in extent and as yet very incompletely known. The three main subformations are:

(i) Those dominated by *Argyrodendron* spp., *Dysoxylum fraseranum*, and and *Elaeocarpus grandis*.

(ii) Those dominated by *Ceratopetalum apetalum*. .

(iii) The "dry scrub" communities.

Ideally all formations and their subdivisions should be defined only on their physiognomic characters, but in the case of rain-forests historical influences have given them names implying certain environmental features and it would be unprofitable at this stage to alter these well-established, though in some ways undesirable, names. Thus Beadle and Costin (1952) define the tropical, subtropical, temperate, and monsoon subformations in Australia, while Richards (1952) writing about the tropical rain-forest in its truly climatic sense, mentions also the seasonal evergreen, montane, and submontane rain-forests.

Three of the above terms are applicable to the local communities mentioned above, but a new combination seems necessary for the dry scrubs, and the name "dry rain-forest" is suggested. The four main subformations occurring in New South Wales thus are:

(i) *Tropical Rain-forest*.—Communities characterized by three tree layers, very common buttressing, with lianes and vascular epiphytes fairly common. The *Argyrodendron*, *Elaeocarpus grandis*, and *Dysoxylum* communities fall into this category. These locally represent a very marginal form of tropical rain-forest, as

is indicated by the absence of cauliflory, the limited number of species, the relatively small leaves, and the tendency to dominance by a few species.

(ii) *Subtropical Rain-forest*.—Communities showing two tree layers, the upper one forming a fairly continuous canopy; rare buttressing, and lianes and vascular epiphytes present but seldom common. The northern *Ceratopetalum* communities, and also the communities from Barrington and the Illawarra scarp conform to this description.

(iii) *Temperate Rain-forest*.—Communities with a dense, deeply canopied upper storey and a scattered second storey, buttressing practically absent and lianes rare. *Nothofagus* communities are the oft-quoted examples of this subformation, which barely fits Beadle's and Costin's definition of rain-forest since lianes and sometimes vascular epiphytes are rare or absent; indeed Warming (1909) likens its structure to that of the northern spruce forests.

(iv) *Dry Rain-forest*.—Communities with two tree layers, the upper one scattered and containing mainly deciduous or xerophytic species; buttressing rare, heavy lianes common, and vascular epiphytes usually not common. These communities have been studied in Queensland by Blake (1941), who regards them as monsoon forest (Blake 1940), or in the terminology of Beadle and Costin, monsoon rain-forest. However, they differ quite markedly from Schimper's (1935) illustrations of the Burmese monsoon rain-forests, where large, deciduous trees clearly dominate the entire stand, while the second storey of trees is far more open than in Australia. Hence the new term seems warranted.

Of the other stands summarized in Table 4, the Bruxner Park community, a typical "gully rain-forest", is structurally intermediate between the tropical and subtropical subformations. The Moore Park community is intermediate between the tropical and dry rain-forests: it is characteristic of the gallery forests once common along watercourses in the drier parts of the Richmond River valley, and further study will probably show it to deserve subformation status. Similarly the Coff's Harbour headland stand, typifying a littoral community common on the North Coast, should ultimately be put into a distinct subformation. The curious Mt. Lindsay *Schizomeria–Banksia* community is the only such community so far recorded in New South Wales; it clearly represents a local adaptation to extraordinary environmental conditions, and appears to be structurally related to the montane rain-forests.

Mr. L. J. Webb of the Division of Plant Industry, C.S.I.R.O., Brisbane (personal communication), has recently made an exhaustive study of eastern Australian rain-forests. He considers temperate rain-forests to be a synonym for montane rain-forest, and does not recognize the presence of tropical rain-forest outside of north Queensland. He regards the communities here called tropical as being subtropical, while the subtropical rain-forests of this review become submontane rain-forests. His arguments have much weight, and there is clearly a case for standardization of terms. In the meantime the names used here, particularly in relation to the stands dominated by *Ceratopetalum* and *Nothofagus*, are preferred on the grounds of established usage.

Besides needing standardizing, the classification given here also requires amplification. However, it does allow the appearance of the main rain-forest stands

to be readily understood, and at the same time broadly groups communities whose silvicultural characters might be expected to be similar. This in turn offers a handy approach to solving the problems associated with applying forest management to these stands.

V. Rain-forest Floristics

The floristic classification of New South Wales rain-forests is still very incomplete, owing to the scanty information on the species composition of the various communities, and the almost complete absence of any frequency studies on the subject. However, a rudimentary classification can be made, and is shown in a summarized state in Table 5. This is likely to be considerably altered and enlarged as more information becomes available, but in the meantime it should act as a useful basis for later work.

Six alliances, as defined by Beadle and Costin (1952), and a number of associations appear clearly marked.

(*a*) Nothofagus moorei *Alliance*

The temperate rain-forest found in cool moist sites from Barrington in the south to the McPherson Ranges. North of the Hastings River *Ceratopetalum* is almost invariably present as an important associate, but at Barrington *Nothofagus* is apparently the sole tall tree species (Fraser and Vickery 1938). Thus two associations can be recognized, depending on the presence or absence of *Ceratopetalum* in the upper storey. A species list for the alliance from Barrington is given by Fraser and Vickery.

(*b*) Ceratopetalum apetalum *Alliance*

A subtropical rain-forest, and economically the most valuable of the rain-forest alliances. In the north it is confined to areas of high rainfall and relatively poor soils, but in the south it encroaches on to the richer soils. A number of distinct associations can be recognized. In some of these *Ceratopetalum* itself is absent but its common associates dominate the stand. This suggests that these associations should be included in the alliance. The associations so far recognized are:

(i) Ceratopetalum–Schizomeria *Association*.—The typical North Coast form, in which *Schizomeria ovata* is usually the second most common tree. Species lists for Moonpar State Forest and the Hastings River Catchment are given respectively in Appendix I and by Burges and Johnston (1953).

(ii) Ceratopetalum–Doryphora *Association*.—Discussed by Brough, McLuckie, and Petrie (1924) from Mt. Wilson, where there is a strong Antarctic element in the associated species. A very similar community occurs at Styx River State Forest, east of Armidale, where the *Nothofagus* alliance occurs also. A species list is given by the Mt. Wilson authors.

(iii) Schizomeria–Doryphora–Ackama–Cryptocarya glaucescens *Association*.—The Barrington community from which *Ceratopetalum* itself is absent. A species list is given by Fraser and Vickery (1938).

TABLE 5

RAIN-FOREST FLORISTIC GROUPS IN NEW SOUTH WALES

Subformation	Alliance	Association	Typical Locality	Remarks
Temperate	*Nothofagus moorei*	(i) *Nothofagus moorei*	Barrington	
		(ii) *Nothofagus–Ceratopetalum*	Mt. Banda Banda	
Subtropical	*Ceratopetalum apetalum*	(i) *Ceratopetalum–Schizomeria*	Moonpar S.F.*	Typical North Coast form
		(ii) *Ceratopetalum–Doryphora*	Mt. Wilson	
		(iii) *Schizomeria–Doryphora–Ackama–Cryptocarya glaucescens*	Barrington	
		(iv) *Ceratopetalum–Diploglottis*	Bulli	Also allied to *Argyrodendron* alliance
		(v) *Doryphora–Acacia melanoxylon*	Robertson	Degenerate form
		(vi) *Sloanea woollsii*	Bruxner Park	Linking with *Argyrodendron* alliance
Tropical	*Argyrodendron* spp.	(i) *Argyrodendron* spp.	Wiangarie S.F.	
		(ii) *Dysoxylum fraseranum*	Tooloom	Higher altitudes
		(iii) *Elaeocarpus grandis*	Whian Whian S.F.	Along creeks in associations (i) and (iv)
		(iv) *Cedrela–Flindersia* spp. (?)	Whian Whian S.F.	Big Scrub rain-forest
Dry	*Hemicyclia australasica*	(i) *Araucaria cunninghamii*	Mt. Pikapene S.F.	
		(ii) *Brachychiton discolor*	Koreelah	More adverse conditions
"Littoral"	*Cupaniopsis anacardioides*	(i) *Cupaniopsis anacardioides*	Pine Creek S.F.	Behind beach dunes
		(ii) *Tristania conferta*	Coff's Harbour	Exposed headlands
"Gallery"	*Castanospermum australe*	(i) *Castanospermum australe*	Moore Park	
		(ii) *Eugenia ventenatii*	Myrtle Creek	
"Montane"	?	(i) *Schizomeria–Banksia integrifolia*	Mt. Lindsay	

*S.F. = State Forest.

(iv) Ceratopetalum–Diploglottis *Association.*—The South Coast form, which has many features of the tropical subformation and many species from the *Argyrodendron* alliance. Neither species used to name the association is necessarily a true dominant, but both are usually present, are quite distinctive, and represent typical species from the two alliances whose mixture forms the association. Davis (1941) gives a species list for the association.

(v) Doryphora–Acacia melanoxylon *Association.*—The degenerate community from Robertson, mentioned by Phillips (1947). It possibly represents a *Ceratopetalum–Doryphora* or *Ceratopetalum–Diploglottis* association considerably altered by man's activities.

(vi) Sloanea woollsii *Association.*—The fairly common North Coast "gully rain-forest", which is both structurally and floristically intermediate between the *Ceratopetalum* and *Argyrodendron* alliances. Both of the species giving their names to these alliances are frequently present, but *Sloanea woollsii* is generally the dominant species in the stand. A list of species from Bruxner Park is given in Appendix I.

(*c*) Argyrodendron *spp. Alliance*

A tropical rain-forest found on good soils north of the Comboyne Plateau, with its floristic influence felt south of Sydney. In all areas it is extremely luxuriant, and floristically very rich and varied. The two *Argyrodendron* spp., *A. trifoliolatum* and *A. actinophyllum*, either together or separately, are frequent and distinct species throughout the alliance. The selection of true dominants is very hard owing to the difficulty in telling which floristic changes are due to chance, and which to environment. However, three or possibly four associations can be distinguished: the *Argyrodendron* association, in which one or both of the above species are the commonest dominants; the *Dysoxylum fraseranum* association, found in the more elevated and cooler areas, with *Dysoxylum* becoming the commonest dominant; the *Elaeocarpus grandis* association, found as narrow bands along creeksides within the *Argyrodendron* association; and possibly a fourth, in which *Cedrela toona* and *Flindersia* spp. were originally common, occupying the rich Big Scrub area on the lower Richmond and Tweed Valleys. The *Elaeocarpus* association also occurs within this last association. Species lists for the first two associations from Wiangarie State Forest and Tooloom Plateau are given in Appendix I. The *Sloanea woollsii* and *Ceratopetalum–Diploglottis* associations link this alliance to the *Ceratopetalum* alliance.

(*d*) Hemicyclia australasica *Alliance*

Structurally a dry rain-forest in which a scattered overstorey of *Araucaria cunninghamii*, *Flindersia* spp., *Brachychiton discolor*, and other species is usually present. The main, low level storey is marked by a family dominance of the Sapindaceae and Euphorbiaceae, rather than of any individual species: however, *Hemicyclia* was chosen to name the alliance as it is one of the most frequent and constant members of the community. The alliance is found in usually somewhat sheltered sites in the drier areas north of the Clarence River. It appears identical with the

Araucaria subclimax of Cromer and Pryor (1942) and the Stanley Basin communities studied by Blake (1941), both from southern Queensland. Two associations can be recognized based on the overstorey species: in better areas the overstorey is less scattered and contains much *Araucaria*, while in more adverse sites the deciduous *Brachychiton* is the only tall species common. A species list for the *Araucaria* association at Mt. Pikapene State Forest is given in Appendix I.

(*e*) Cupaniopsis anacardioides *Alliance*

The small patches of rain-forest occurring commonly along the coast north of Sydney. Two associations can be recognized: *Cupaniopsis anacardioides* association, found along tidal estuaries and behind the coastal sand-dunes; and *Tristania conferta* association, clearly dominated by windswept specimens of this widespread species, on the more exposed headlands. Osborn's and Robertson's (1939) rain-forest stands on the Myall Lakes belong to this alliance.

(*f*) Castanospermum australe *Alliance*

A riverbank community of the drier areas, and apparently confined to land north of the Clarence River. Again two associations occur, the fairly rich *Castanospermum australe* association, for which the species list from Moore Park is given in Appendix I, and the species-impoverished *Eugenia ventenatii* association of the less favourable localities. The *Castanospermum* association is recognized by Cromer and Pryor (1942) as the *Castanospermum–Grevillea robusta* association.

(*g*) Others

There is finally the wind-dominated *Schizomeria–Banksia integrifolia* association from Mt. Lindsay. This is clearly a distinct association which, being derived from the *Argyrodendron* alliance, should probably be included in that alliance. It is, however, both structurally and floristically distinct from all other communities.

VI. Factors Affecting Rain-forest Distribution

Although Clement's monoclimax theory, with its emphasis on climate, dominated Australian ecological thought for a considerable period, it is now recognized that a number of environmental factors are responsible by their interaction for determining the distribution of vegetation. This view is in keeping with that of Jenny (1941) on the formation of soil. Not all authors agree about the actual factors concerned, but probably five are involved—climate, soil, topography, history, and the biotic factor. Each of these in turn is made up of a number of components. Theoretically this leads to the recognition of five types of climax community, depending upon which factor limits the further development of the community. In practice considerable difficulties are found in attempting to identify these climaxes, and it may be doubted if there is any purpose in the attempt.

The effects of these factors on rain-forest distribution in New South Wales are considered in detail below.

(a) *Climatic Factor*

Four main components of the climatic factor can be recognized; temperature, light, water, and wind. Each of these, like other environmental factors, acts on the individual species in the community. As the components vary, the community undergoes a sifting and some species are added to the community, others are lost. It is this sifting effect which ultimately determines the distribution of vegetation. Its importance has been stressed by Herbert (1935).

Temperature in itself can have little effect on the broad distribution of rain-forest, since rain-forest covers a very wide range of temperature conditions in New South Wales. Most localities experience occasional summer days when the temperature exceeds 100°F, while all but the most maritime situations receive winter frosts. The higher altitude rain-forests, which include the *Nothofagus*, *Dysoxylum*, and *Ceratopetalum–Schizomeria* associations, have very severe and lengthy winters, and periodically receive snowfalls. The rain-forest canopy greatly modifies these extreme conditions within the community, but it is common experience that logging activities, by opening the canopy of the stand, cause the gradual deterioration and in some cases ultimate death of the remaining stems in the elevated rain-forests. It is possibly due to some similar cause that the Robertson rain-forest is stated by Phillips (1947) to be in the process of invasion by eucalypts.

Fraser and Vickery (1938) suggest that warmth limits the lower boundaries of the *Nothofagus* association, whilst cold probably limits the upper boundaries of the subtropical rain-forests where these border the *Nothofagus* association. However, the main effects of temperature appear to be in limiting the range of many species along the New South Wales coast. This effect is clearly shown by the gradual impoverishment in species of the rain-forest communities from north to south; its importance has been stressed by Francis (1951), while de Beuzeville's (1943) study of the climatic tolerance limits of various species shows the mechanics rather well.

Openings in the higher-altitude rain-forests develop into frost hollows which have an economic importance exemplified by the failure of attempts to establish *Araucaria* plantations on the Dorrigo Plateau. The cold in such openings appears also to be the reason for the perpetuation of the grasslands at Clouds Creek; only in the rare sequence of relatively warm winters can *Eucalyptus saligna* regeneration become established around the edges of the clearings, and then subsequently the *Argyrodendron* association moves in under shelter of the eucalypts.

Light, like temperature, has little effect on the overall distribution of rain-forest in New South Wales. It does, however, have one important effect; low light intensities within the rain-forest direct the course of succession to a community of species which can either ecesize in these low light conditions, or else establish themselves during the occasional brief periods when gaps occur in the canopy. It thus tends to prevent the establishment of the light-demanding eucalypts within the rain-forest, and so precludes the invasion by sclerophyll forest of any but the most degenerate rain-forest communities, such as the Robertson community of Phillips (1947). Evidence for the invasion of healthy rain-forest by eucalypts, such as that presented by Brough, McLuckie, and Petrie (1924) for the Mt. Wilson *Ceratopetalum–Doryphora* association, must be viewed very critically.

Atmospheric water in its various forms affects plant growth in two ways, either by supplying moisture for growth in such forms as rain, snow, dew, and mist, or by influencing the rate of transpiration, a humidity effect. Rain-forest apparently needs constantly high humidities, but provided soil moisture is adequate the communities can maintain their own high humidities within the canopy (Richards 1952). Trees from the upper storeys must be able to tolerate wider humidity variations, and where a protracted dry season is experienced it is noteworthy that many of the taller trees tend to be xeromorphic (e.g. *Araucaria*) or deciduous (e.g. *Brachychiton*). These features are well shown by the dry rain-forests, as well as by certain rain-forest–margin communities. Indeed the close floristic and structural similarity between the *Hemicyclia* alliance in northern New South Wales and the *Araucaria* subclimax of Cromer and Pryor (1942) in Queensland has already been noted. Dry rain-forest is apparently maintained as a climax community by reason of a seasonal period of low humidity, which in turn is dependent on a long annual drought (see monthly rainfall averages for Mt. Pikapene State Forest, Table 2).

The high internal humidities of the rain-forest provide almost nightly dewfalls, which supply a regular source of water to the non-vascular epiphytes. Constant mists, a feature of many rain-forest localities, are of more importance in relation to rain-forest distribution. The dense moss growth found towards the upper rain-forest levels on Mt. Lindsay appears to owe its existence to the frequent cloud which enshrouds the mountain, whilst the restriction of temperate rain-forest to cool sites commonly fogbound suggests the importance of mist in determining the limits of the *Nothofagus* alliance, probably by acting on the transpiration rate. Snow is too infrequent to be of any importance as a water supplier to the rain-forest economy.

The early recognition of the importance of rainfall to rain-forest distribution is reflected in the very name of the formation. It is true that, under favourable edaphic and topographic conditions, rain-forest is found in areas where rainfall is less than 40 in. yearly, or where there is a long and severe dry season. However, it only becomes a dominant feature on undulating land where the rainfall exceeds 60 in. per annum, and possibly slightly less towards the south. This is clearly shown by studying the rainfall map of New South Wales (Commonwealth Bureau of Meteorology 1948) on to which the isohyets of Fraser and Vickery (1937) for the Barrington area have been added (Fig. 3). Six regions have rainfalls in excess of 60 in.: the Kosciusko region, with its alpine and subalpine climate, and the five major rain-forest areas previously mentioned.

The influence of rainfall is well shown by the vegetation series on Mt. Lindsay. Here on a single slope and on soils derived from the one parent material, but under conditions of rainfall clearly increasing with elevation, the series runs from tall woodland at the valley bottom through wet sclerophyll forest to tropical rain-forest. The absence of dry sclerophyll forest from this and other areas of similar soil in the district suggests that this subformation may be edaphically controlled.

The *Nothofagus* alliance is normally confined to areas where rainfall exceeds about 70 in. per annum and where frequent mists lower the transpiration rate. Outside this rather restricted zone *Nothofagus moorei* itself occurs as a creek-bank species: this is just one example of a rain-forest community existing under lower

rainfall conditions than would usually be expected. It is brought about by local edaphic or topographic conditions compensating for the lower precipitation, and it suggests that rainfall tolerance limits for species such as are given by de Beuzeville (1943), may not have much meaning.

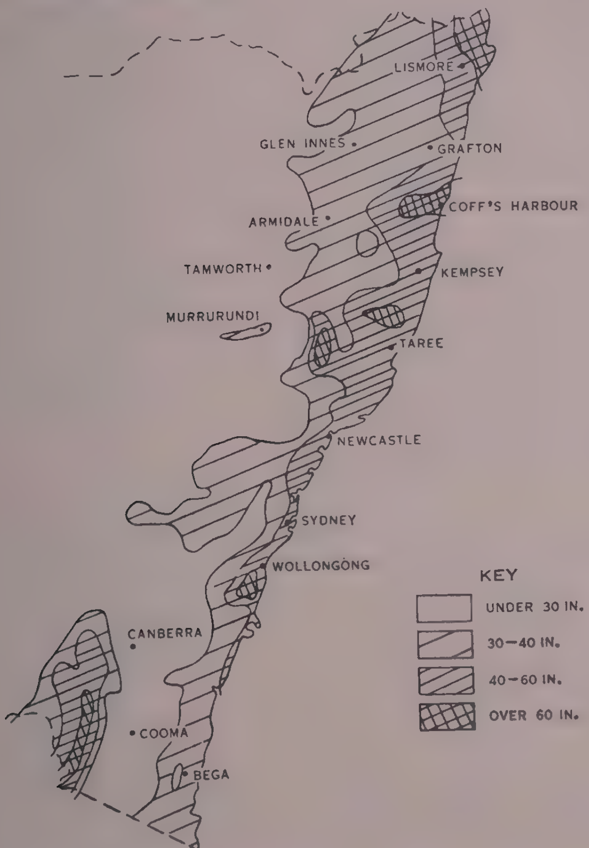

Fig. 3.—Rainfall distribution in New South Wales

Winds, in their effects on vegetation, can be desiccating, constructive, or destructive. All three effects can be found in New South Wales rain-forests, and, as would be expected, the wind factor is closely allied to the topographic factor. Desiccating winds in this state are those from the north and west and their effect is the restriction of rain-forest, outside the five main areas, to regions sheltered from these directions. Even in the high rainfall areas westerly slopes frequently do not carry rain-forest.

Constructive winds are those bringing regular supplies of moisture, and in some cases plant nutrients, to the rain-forest communities. Excluding the rain-bearing winds the main influence here is with the *Cupaniopsis* alliance, which appears to receive a degree of moisture, whose main effect is to lower transpiration, from the

winds blowing almost continually off the sea, thus allowing rain-forest growth in areas with a lower rainfall than that normally required by rain-forest. The same winds bring in certain chemical elements, notably sodium and phosphorus, to the plant community. Abnormally high contents of both these elements can be found in plants collected from maritime stations, and the composition of these coastal rain-forests is probably limited by their tolerance to perpetual wind, with its strong shearing effect, and by their ability to withstand very high sodium concentrations.

Shearing is one of the destructive effects of wind. It occurs not only along the coast but also in other exposed regions, and seems mainly responsible for the low height of the *Schizomeria–Banksia* association on Mt. Lindsay. Cyclones have little effect on the nature or distribution of rain-forests in New South Wales, though "hurricane forests" (communities perpetually deficient in large trees) have been reported from overseas (Beard, quoted by Richards 1952). In New South Wales the occasional tropical cyclone will destroy overmature trees and allow regrowth to develop, and may in rare cases fell all trees over relatively extensive areas. During the cyclone of February 1954 in the northern part of the State, openings totalling about 200 acres were made in an *Argyrodendron* alliance in Yabbra State Forest, near Bonalbo, and it is thought that similar cyclone destruction, followed by fire, may have originated the Clouds Creek grasslands.

(*b*) *Edaphic Factor*

It is not intended to review here all the effects that soil can have upon vegetation though many of these doubtlessly influence the New South Wales rain-forests in various ways. Local rain-forests occur on soils which vary in texture from sands behind many beaches to clays derived from shales and basalt (see Table 6). Rain-forest appears only on sands where there is an ample supplementary supply of soil moisture, while the rain-forest clay soils are notable for their very good structure. Heavy texture, which in more southern regions has been regarded as the cause of treeless areas on basalt soils (Cambage 1918; Patton 1930), certainly does not interfere with rain-forest development and is definitely not the cause of the Clouds Creek grasslands, as Cambage infers. Dry rain-forest is confined to heavy textured soils, probable due to their high water-holding capacity.

The same reason appears to account for the situation at Clouds Creek, where *Ceratopetalum* is restricted to the gullies, with wet sclerophyll forest on higher topographic positions on the same soil parent material (shale), while a nearby elevated basalt pocket supports *Argyrodendron*.

Under New South Wales conditions soil nutrients can be shown to exert a profound influence on rain-forest distribution. In Table 6 soil contents of phosphate and certain exchangeable cations are shown. Phosphate was determined by a method similar to that described by Beadle and Tchan (1955), the cations were extracted by the leaching apparatus described by Black (1947), and the content of calcium, potassium, and sodium was determined on an EEL Flame Photometer. Appendix II shows the amounts of these same ions in the ash of various plants.

Sodium is not generally regarded as an essential plant nutrient, but is invariably present in plant ash in measurable quantities. *Eugenia smithii*, *Eucalyptus* spp., and

TABLE 6

SOIL ANALYSIS RESULTS

Locality	Parent Material	Texture*	Total PO_4 (p.p.m.)	Exch. Bases	Na	K	Ca
				(m-equiv/100g)			
Rain-forest—*Argyrodendron* alliance							
Lamington N.P.	Basalt	Cy L	2940	15·8	0·5	0·8	10·5
Whian Whian S.F.	Basalt	Cy L	6200	25·9	0·8	1·7	21·9
Tooloom Plateau	Basalt	Cy L	7620	62·0	0·6	1·9	47·2
Tooloom Plateau (cleared)	Basalt	—	6720	47·2	0·6	2·8	37·6
Lynches Creek	Basalt alluvium	—	3930	—	—	—	—
Wiangarie S.F.	Basalt	—	3960	—	—	—	—
Clouds Creek S.F.	Basalt	—	5120	—	—	—	—
Rain-forest—*Ceratopetalum* alliance—*Ceratopetalum–Schizomeria* association							
Lamington N.P.	(acid igneous)	Sl Cy	520	5·1	0·6	0·8	3·5
Whian Whian S.F.	(acid igneous)	Sl Cy L	—	4·4	—	—	—
Whian Whian S.F.	(acid igneous)	—	630	2·3	0·1	0·6	1·1
Whian Whian S.F.	(acid igneous)	—	480	—	—	—	—
Brooklana	Shale	Cy L	1090	3·6	0·4	1·0	1·8
Orara West S.F.	Shale	Cy L	1070	11·3	—	—	—
Dome Mountain	Shale	Cy L	840	—	—	—	—
Rain-forest—*Ceratopetalum* alliance—*Sloanea woollsii* association							
Bruxner Park	Shale alluvium	Cy L	1290	—	—	—	—
Rain-forest—*Ceratopetalum* alliance—*Ceratopetalum–Doryphora* association							
Mt. Wilson	Basalt	Cy L	3180	—	—	—	—
Rain-forest—*Ceratopetalum* alliance—*Ceratopetalum–Diploglottis* association							
Gosford	Shale alluvium	Sd L	510	5·0	0·2	0·2	3·5
Rain-forest—*Hemicyclia* alliance							
Unumgar S.F.	Basalt	Cy	2940	—	—	—	—
Koreelah	Basalt	Cy	3040	55·8	—	—	—
Mt. Pikapene S.F.	Basalt	Cy	2420	68·1	—	—	—
Rain-forest—*Cupaniopsis* alliance							
Pine Creek S.F.	Beach sand	Sd	650	16·0	—	—	—
Wet sclerophyll forest							
St. Ives	Shale	Cy	960	6·8	0·4	0·9	2·3
Gosford	Shale	Cy L	770	10·2	0·3	0·7	5·9
Lynches Creek	Shale (?)	—	1680	—	—	—	—
Whian Whian S.F.	Volcanic (?)	—	1710	—	—	—	—
Barcoongere S.F.	Shale		510	9·0	0·3	0·5	4·9
Bruxner Park	Shale	—	720	—	—	—	—
Dome Mountain	Shale	—	1050	—	—	—	—
Tall woodland							
Mt. Pikapene S.F.	Basalt	—	1580	—	—	—	—
Dry sclerophyll forest							
Barcoongere S.F.	Shale	—	110	0·9	0·1	0·1	0·4
Wet mallee							
Lamington N.P.	Obsidian	Sl L	226	4·5	—	—	—
Grassland							
Clouds Creek S.F.	Basalt	—	3380	—	—	—	—

*Cy, clay; L, loam; Sd, sand; Sl, silt.

Wilkiea huegeliana contain characteristically high quantities of sodium (in *Eugenia smithii* sodium regularly makes up about 5 per cent. of the total weight of ash), while some, though not all, other species show locally high values when exposed to constant salt-bearing winds. The very high value for sodium in *Wilkiea* from Coff's Harbour is due to crystalline salt on the outside of the leaves. Sodium is mainly deposited in the soil from wind-blown ocean spray, and its chief effect on rain-forest distribution might be expected to be in locally limiting the growth of plants which cannot tolerate high concentrations of the ion, while conversely the composition of the coastal *Cupaniopsis* communities must be largely determined by a tolerance of the constituent species to high values of sodium.

TABLE 7

SOIL NUTRIENT LEVELS FOR VARIOUS COMMUNITIES

Community	Exch. Cations (m-equiv/100g)	Exch. Ca (m-equiv/100g)	Exch. K (m-equiv/100g)	Total PO_4 p.p.m.
Argyrodendron alliance	15·8–62·0	10·5–47·2	0·8–2·8	2940–7620
Ceratopetalum–Schizomeria association	2·3–11·3	1·1–3·5	0·6–1·0	520–1090
Sloanea and *Ceratopetalum–Diploglottis* associations	5·0	3·5	0·2	510–1290
Ceratopetalum–Doryphora associations				3180
Hemicyclia alliance	55·8–68·1			2420–3040
Wet sclerophyll forest	6·8–10·2	2·3–5·9	0·5–0·9	480–1710
Dry sclerophyll forest and wet mallee	0·9–4·5	0·4–3·2	0·1–0·9	110–226

The other three nutrients are regarded as essential for plant growth. Apart from certain individual peculiarities, such as the very low calcium contents of *Orites*, the calcium and potassium contents of plant ash show a fairly general relationship to the total ash content, species with much ash having high levels of calcium and potassium. This relationship does not hold for phosphorus, some species with much ash having relatively low phosphorus contents (e.g. some samples of *Claoxylon*), while some species with very little ash can have high phosphorus levels (e.g. *Pinus*, *Eucalyptus gummifera*).

Extending this comparison, the various nutrients in the leaf can be compared with the same nutrients as they occur in the soil at the site whence the leaf was collected. No relationships can be observed in such a comparison between exchangeable cations and plant ash, exchangeable potassium and plant potassium, or exchangeable calcium and plant calcium. With phosphorus, however, a distinct relationship between leaf phosphorus and total soil phosphorus can be recognized. This is best shown by individual species (e.g. *Ceratopetalum*, *Claoxylon*, *E. gummifera*), but all species lumped together clearly show the same trend. At two sites, Pine Creek and Gosford, leaf phosphorus is higher than would be expected from the soil values. The Pine Creek leaf values are due to sea spray constantly supplying phosphate from

the sea, and bear no relationship to the soil levels, while at Gosford the soil analysed was sandy, and probably represents a recent deposition of coarse alluvium in which phosphorus and other nutrients have yet to be accumulated by the vegetation.

Finally the range of values of the soil nutrients was tabulated according to the type of community they support (Table 7).

This table is based on relatively few determinations, but enables some general conclusions to be made. Firstly, low soil levels of phosphorus are usually associated with low levels of other nutrients, thus obscuring the identity of the limiting nutrient. Certain communities are confined to soils with definite nutrient characteristics; *Argyrodendron* and *Hemicyclia* alliance soils are plentifully supplied with bases and phosphorus, as are the *Ceratopetalum* alliance soils derived from basalt (*Ceratopetalum–Doryphora* and some *Ceratopetalum–Diploglottis* association soils). The *Ceratopetalum–Schizomeria* association in northern New South Wales and the wet sclerophyll forests which were studied are on soils with much lower levels of the nutrients, both communities occurring over the same range of values. The dry sclerophyll forest and wet mallee soils are even lower in nutrients.

The major difference between phosphorus and the two cations is their behaviour in the plant. Calcium and potassium occur over a limited range of values in any particular species, and their contents in the plant do not tend to increase with rises in the soil level. The reverse is true of phosphorus; its range of value in any species is high, and is related to the amount of phosphorus in the soil (or for maritime sites, the spray). This suggests that phosphorus is a true limiting factor, and all that is in the soil is utilized by the plant. Partial support for this theory is provided by those species, notably *Pinus elliottii* and *Eucalyptus gummifera*, which have been sampled from soils covering a wide range of nutrient levels. As before, calcium and potassium in the leaf are at relatively constant levels, whilst leaf phosphorus increases greatly with increasing soil phosphate. In the case of *Pinus*, it can be shown that leaf phosphorus also bears a close relationship to site quality, a measure of the inherent fertility of the soil.

The theory of the limiting nature of phosphorus is particularly helpful in explaining certain features of the distribution of rain-forest and associated vegetation types in New South Wales.

In northern New South Wales, soils containing between about 500 and 1200 p.p.m. PO_4 will, under favourable climatic and topographic conditions, support a subtropical *Ceratopetalum–Schizomeria* association; where conditions are locally more arid the vegetation becomes wet sclerophyll forest. As the PO_4 content increases above 1200 p.p.m. the structure of the rain-forest becomes increasingly tropical and *Ceratopetalum* loses its dominance, and finally disappears from the community, which becomes dominated by *Argyrodendron* or *Dysoxylum*. Even under the highest soil phosphate regimes the more arid sites will carry wet sclerophyll forest (e.g. below the rain-forest margin on Mt. Lindsay and at Wiangarie State Forest). Under still more xeric conditions at high soil phosphate levels the vegetation is of tall woodland (e.g. Mt. Lindsay, Mt. Pikapene). Wet sclerophyll forest possibly exists at somewhat lower phosphate levels than the *Ceratopetalum–Schizomeria* association,

but below 300 p.p.m. (and probably even higher) it is replaced by dry sclerophyll forest or wet mallee. As seen at Lamington National Park the *Ceratopetalum* rain-forest can border directly on to the mallee formation, without any intervening wet sclerophyll forest band.

Towards southern New South Wales the *Ceratopetalum* alliance occurs on soils with much higher phosphate levels. This can be explained on grounds of competition. Under the more favourable climatic conditions of the north competition for space is very active and *Ceratopetalum* and its associates are restricted to the less fertile soils. Where soil phosphate is higher, other species, which owing to their phosphate tolerance limits are unable to grow successfully at lower levels, enter the community and squeeze *Ceratopetalum* out. When competition is relaxed, *Ceratopetalum* is very successful on these soils, as can be seen from isolated trees and plots planted on such sites. However, climatic sifting tends to remove many of the most successful competitors from these more fertile soils towards the south. With this release of competitive pressure *Ceratopetalum* is able to encroach on to these soils, and may even dominate the stand (e.g. Mt. Wilson). On other sites where the climate is less severe the remaining species typical of the tropical rain-forest still hold *Ceratopetalum* in check, so that though present it does not truly dominate the stand (*Ceratopetalum–Diploglottis* association). A similar occurrence of *Ceratopetalum* on the more fertile soils is found at the altitudinal limits of rain-forest, where *Ceratopetalum* is associated with *Nothofagus* on soils derived from basalt (e.g. Mt. Banda Banda and the gullies of the high western Dorrigo Plateau).

Like *Ceratopetalum*, *Nothofagus* and its temperate rain-forest associates appear to be fairly tolerant of low phosphate contents. The *Hemicyclia* alliance is confined to soils derived from basalt and rich in nutrients. However, whilst the soil nutrients doubtlessly determine to some extent what species will be present, the occurrence of the community appears to be more strongly related to topographic and soil physical conditions.

Whilst it is not claimed that phosphate in the soil is the only nutrient influencing the nature and distribution of rain-forest in New South Wales, it does seem clear that phosphate does exert a very great influence on the local coastal vegetation, and particularly on rain-forest.

The various soil characteristics, both chemical and physical, are closely related to the soil parent material. Of the various parent materials, basalt appears the most favourable for the development of rain-forest, since it gives well-structured soils of heavy texture and high phosphate content. On such soils the most luxuriant types of rain-forest develop, and rain-forest grows well, beyond what would otherwise be its climatic limits. Other rock types also commonly carry rain-forest, though low phosphate values make for a less complex type of community. Excessively drained soils and soils derived from rocks low in nutrients, such as sandstone, will not normally support rain-forest except where there are supplementary supplies of water (e.g. in low topographic positions) or nutrients, the latter provided either by accumulation (e.g. gullies in the Hawkesbury sandstone) or by spray.

(c) *Topographic Factor*

Exposure to atmospheric conditions and the effects of slope are the main influences that topography has on vegetation. Under conditions favourable to rain-forest development, exposure is chiefly related to the presence of desiccating winds, which may determine the local patterns of vegetation. Thus in typical rain-forest country only the most exposed locations carry eucalypts, whereas in marginal rain-forest areas rain-forest can only maintain itself in sites specifically sheltered from the north and west. This can be seen in the *Hemicyclia* dry rain-forest in northern New South Wales, in the *Ceratopetalum–Doryphora* association on Mt. Wilson, and on the high basalt plateaux of Dorrigo and Barrington, where the windswept plateau surfaces carry grassland and stunted snow gums, with *Nothofagus* rain-forest confined to the protected gully floors. Occasionally communities of rain-forest resistant to exposure can be found; the curious *Schizomeria–Banksia* association of Mt. Lindsay is an example.

The influence of slope on rain-forest distribution is exerted through the distribution of water nutrients in the soil. High topographic positions tend to be quickly drained of water and to lose their nutrients rapidly. On lower positions the soils are deeper, they accumulate the nutrients leached from above, and moisture conditions are more favourable. This topographic sequence gives a soil catena whose effect on vegetation is frequently profound, leading to the development of what might be termed a vegetation catena. An example familiar to all foresters in northern New South Wales is the sequence *Eucalyptus paniculata–E. triantha–E. propinqua* on the ridge tops, *E. pilularis–E. saligna* on the slopes, and *E. grandis* or *Sloanea woollsii* association in the gullies. In this case the restriction of rain-forest to the gullies is probably an effect of moisture rather than of nutrients; in the Hawkesbury sandstone gullies, however, nutrients appear more important (Beadle 1954).

The fringing *Castanospermum* alliance is essentially limited in its distribution by topography, occurring in the lower topographic positions where moisture is plentiful.

It will be noted that the effect of the topographic factor always seems to be one of modifying either the climatic or edaphic conditions. For this reason it should perhaps be regarded as a subsidiary factor of distribution, rather than of equal status to soil and climate.

(d) *Historic Factor*

Present-day vegetation patterns have largely developed as the result of past migrations of the flora. This certainly applies to the pattern of rain-forest distribution in New South Wales. The very marked discontinuity of this distribution results from the severe climatic changes of the Pleistocene and Early Recent eras, when the previously existing widespread rain-forest flora was driven northwards by the Ice Age cold and then destroyed over large areas by the Aridity, thus restricting it by and large to its present strongholds. However, in this connection it is worth noting that even under the most favourable climatic conditions it is unlikely that the barren

Clarence and Hawkesbury sandstone plateaux ever supported rain-forest save in scattered gullies.

More recently, with climatic amelioration, rain-forest has again started to extend its boundaries. Examples of rain-forest invading eucalypt forest are common in northern New South Wales, and Cromer and Pryor (1942) discuss examples from southern Queensland. Only where man's activities have disturbed the rain-forest microclimate are there signs of eucalypts invading the rain-forest.

Another historic effect appears to be found in the absence of certain species from localities that seem suitable for their development. This has been suggested as the reason for the absence of *Ceratopetalum* from Barrington, while *Castanospermum australe*, which is well capable of ecesizing under rain-forest localities when introduced to southern localities, appears to be confined to northern New South Wales through some historical accident.

(e) *Biotic Factor*

The three components of the biotic factor are flora, fauna, and man. The first and last are of some importance in their effects on the local rain-forests.

One major effect of flora is due to the tolerance limits of individual species to the various environmental factors, as has been discussed. Allied to this effect is the tolerance of various species to competition which may prevent their growth on sites environmentally suited to them. This appears to explain the distribution of *Ceratopetalum apetalum* which is limited to poor soils in northern New Wouth Wales, where competition is fiercest, but which, owing to the elimination of competitive species by climatic sifting, is able to establish itself on, and even to dominate, the rich basalt soils further south.

Dispersal capacity is another effect of flora on distribution, and seems to be the reason for the continued restriction of *Castanospermum* to northern New South Wales. Planted trees have naturalized themselves in a rain-forest pocket south of Newcastle, but the species is not found naturally south of the Bellinger River, its spread being hampered by its large seeds and pods which are normally water-dispersed.

Man has had a profound effect on rain-forest distribution. Aboriginal influence was exerted, chiefly unintentionally, through the use of fire, which tended to restrict the advance of rain-forest and to favour the growth of sclerophyll forest in sites otherwise suitable for rain-forest. The use of fire has been extended since white settlement, and it is a valuable weapon in maintaining the economically valuable fire-climaxes, such as the *Eucalyptus grandis* association.

Despite their similarity to the Bunya Mountains clearings in Queensland, which Herbert (1938) believes are due to aboriginal activity, there is no evidence that the Clouds Creek clearings are caused by human interference.

Civilized man's influence on the rain-forest has been immense and almost entirely destructive. The area of rain-forest in the state has been reduced by about 50 per cent. in the last 100 years, and the rain-forest has been replaced by grasslands which are maintained by grazing, fire, and cultivation. Most of the remaining area has been logged and frequently left in a fire-susceptible or degenerate state. Scientific management of the natural rain-forest is still in its most rudimentary stages.

VII. Conclusions

This study has dealt with two aspects of the rain-forests of New South Wales. Firstly, an attempt has been made to classify the rain-forest communities in the state, and, secondly, an explanation for the distribution of these communities has been offered in terms of the various factors of distribution.

The classification is tentative, and more detailed study will doubtless show the need for some alterations and further subdivision, particularly in the floristic classification. At the same time the six alliances and the various associations described can all be readily recognized in the field and should serve as reference points for subsequent work.

The structural classification shows the presence of four major subformations in New South Wales, along with two other structural types which probably deserve subformation status: these last two are the littoral communities in the *Cupaniopsis* alliance and the gallery communities in the *Castanospermum* alliance. The four major types have characteristic structures and occur over relatively wide areas. Despite their distinctiveness, however, it is a curious fact that there are no records of any deliberate previous attempts to distinguish between three of these.

The terminology of rain-forest subformations in general is very confused, and the names given to the four local groups, tropical, subtropical, temperate, and dry, should be used in conjunction with the definitions of these groups, and should not be regarded as having any environmental significance. This is different from Richards's use of the term "tropical rain-forest", which he applies to all rain-forests growing under tropical conditions and which includes a number of distinct structural forms, as for example in the five communities studied in British Guiana (Richards 1952, pp. 236–43). Indeed, it would appear desirable to replace in time the current terms by a new set using purely structural characters to distinguish them.

The distribution of rain-forest in New South Wales appears to be primarily determined by the availability of moisture. For rain-forest to develop the average annual rainfall should be over 60 in., or else some supplementary moisture supplies should be provided by favourable topographic or soil conditions. Where the rainfall is markedly seasonal, dry rain-forest results, and the same conditions of periodic low humidity that seem important in producing this community also lead to many rain-forest margins in the north of the State having very similar structural and floristic composition to the dry rain-forests.

Low temperatures and very moist conditions produce temperate rain-forest. In northern New South Wales the tropical and subtropical rain-forests occur under similar climatic conditions but on soils of markedly different fertility, the subtropical stands being restricted to soils with a relatively low phosphate status. This explains the differing successes that have accompanied land utilization experiments in parts of the State. Thus the western part of the Dorrigo Plateau, formerly covered by tropical rain-forest, now carries rich dairy farms; while cleared land on the eastern plateau, which supported subtropical rain-forest, now carries mainly derelict farms.

Tropical rain-forest is restricted to areas north of the Hastings catchment, apparently by temperature, and south of here subtropical rain-forest occurs on the

more fertile soils. The absence of certain of the subtropical community species from the richer soils in the north is apparently due to the intense competition of the species characteristic of the tropical stands.

The general discontinuity of the rain-forest stands throughout the state is the result of past climatic changes, particularly during the Pleistocene and Early Recent periods.

It can be seen that the present distribution of rain-forest is the result of a complex interaction of many environmental factors. Together these produce the State's most complex and most interesting natural plant communities, which furthermore are of considerable economic value. In the past consideration of these communities has been confused by lumping all the rain-forests not dominated by *Nothofagus moorei* together as subtropical. This study shows that this should not be done, and that the rain-forests of New South Wales are themselves very varied, each type having its own particular points of interest and its own potentialities for future management. It is hoped that this study may lead to the introduction of forest management to these stands.

VIII. Acknowledgments

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APPENDIX I

TYPICAL SPECIES LIST FOR NORTHERN LOCALITIES

Species lists for six localities are given in Table 8 below. These localities belong to the following alliances or associations:

Moore Park	*Castanospermum* alliance
Tooloom Plateau	*Dysoxylum* association
Wiangarie State Forest	*Argyrodendron* association
Mt. Pikapene State Forest	*Hemicyclia* alliance
Bruxner Park	*Sloanea woollsii* association
Moonpar State Forest	*Ceratopetalum–Schizomeria* association

Other lists for New South Wales given in the literature are: Mt. Wilson (*Ceratopetalum–Doryphora* association) (Brough, McLuckie, and Petrie 1924); Hastings Catchment (*Ceratopetalum–Schizomeria* association) (Burges and Johnston 1953); Bulli District (*Ceratopetalum Diploglottis* association) (Davis 1941); Barrington Tops (*Nothofagus* alliance and *Schizomeria–Ackama–Doryphora–Cryptocarya* association) (Fraser and Vickery 1938); and Myall Lakes *Cupaniopsis* alliance) (Osborne and Robertson 1939).

The scientific nomenclature of plants other than eucalypts in the present paper is that used by Francis (1951) or, when not included by that reference, by Maiden and Betche (1916).

TABLE 8

SPECIES LISTS

Family and Species	Moore Park	Tooloom Plateau	Wiangarie	Mt. Pikapene	Bruxner Park	Moonpar
Cyatheaceae						
Alsophila leichhardtii			+		+	+
Araucariaceae						
Araucaria cunninghamii				+		+
Cupressaceae						
Callitris macleayanus						+
Podocarpaceae						
Podocarpus elatus	+					
Palmaceae						
Calamus muelleri					+	
Linospadix monostachya		+	+		+	+
Archontophoenix cunninghamii			+		+	
Araceae						
Colocasia macrorrhiza	+		+			
Pothos loureiri			+		+	
Flagellariaceae						
Flagellaria indica			+		+	
Liliaceae						
Cordyline terminalis		+	+	+		
C. stricta						+
Geitonoplesium cymosum		+		+	+	+
Smilax glycyphylla					+	
S. australis	+		+	+	+	+
Rhipogonum discolor			+	+	+	+
R. sp.					+	
Dioscoreaceae						
Dioscorea transversa				+	+	+
Petermannia cirrosa						+

TABLE 8 (*Continued*)

Family and Species	Moore Park	Tooloom Plateau	Wian-garie	Mt. Pikapene	Bruxner Park	Moonpar
Zingiberaceae						
Alpinia coerulea		+			+	
Orchidaceae						
Calanthe veratrifolia			+			
Piperaceae						
Piper novae-hollandae			+			
Ulmaceae						
Celtis paniculata				+		
Trema aspera	+	+				+
Aphananthe philippinensis	+			+		
Moraceae						
Ficus macrophylla	+			+		
F. watkinsiana		+	+	+	+	
F. stephanocarpa	+					
Cudrania javanensis	+	+		+		
Malaisia tortuosa				+	+	
Pseudomorus brunoniana				+		
Urticaceae						
Laportea gigas		+	+	+		
L. photiniphylla				+		
Proteaceae						
Helicia youngiana						+
Orites excelsa			+		+	+
Grevillia robusta	+			+		
Embothrium pinnatum						+
Stenocarpus sinnuatus					+	
S. salignus						+
Ranunculaceae						
Clematis sp.	+				+	+
Menispermaceae						
Stephania hernandifolia	+					
Legnephora moorei	+			+		
Winteraceae						
Drimys dipetala		+			+	+
Anonaceae						
Melodorum leichhardtii		+	+	+		
Eupomatiaceae						
Eupomatia laurina		+	+			+
Monimiaceae						
Doryphora sassafras			+		+	+
Daphnandra micrantha	+	+	+			
Wilkiea huegeliana			+		+	+
W. macrophylla			+			
Hedycarya angustifolia		+				
Palmeria scandens			+			+
Lauraceae						
Cinnamomum virens		+			+	+
C. oliveri			+		+	

TABLE 8 (*Continued*)

Family and Species	Moore Park	Tooloom Plateau	Wian-garie	Mt. Pikapene	Bruxner Park	Moonpar
Lauraceae (*continued*)						
Litsea zeylanica		+	+			
L. dealbata	+	+	+		+	+
L. reticulata		+	+		+	+
Beilschmiedia obtusifolia	+	+	+		+	
B. elliptica	+		+		+	
Cryptocarya patentinervis					+	+
C. obovata	+		+		+	
C. glaucescens					+	+
C. microneura		+			+	+
C. erythroxylon		+	+			
C. triplinervis	+	+				
C. meissneri						+
Endiandra introrsa						+
E. crassiflora						+
E. muelleri	+				+	+
E. pubens			+			
Capparidaceae						
Capparis nobilis	+	+	+	+	+	
Escalloniaceae						
Quintinia verdonii			+			+
Polyosma cunninghamii			+		+	+
Anopterus macleayanus						+
Pittosporaceae						
Pittosporum undulatum		+				
P. revolutum	+					+
Hymenosporum flavum	+		+		+	
Citriobatus multiflorus	+	+	+	+		+
C. pauciflorus		+				
Billardiera scandens						+
Cunoniaceae						
Callicoma serratifolia					+	+
Ceratopetalum apetalum					+	+
Schizomeria ovata					+	+
Ackama paniculata			+		+	+
Geissois benthami			+		+	+
Leguminosae						
Acacia maideni				+		
A. sp.						+
Pithecellobium pruinosum	+			+		
P. grandiflorum			+			+
Cassia laevigata				+	+	
Erythrina vespertillio				+		
Lonchocarpus blackii				+	+	
L. sp.			+			
Derris scandens		+	+			
Castanospermum australe	+					

TABLE 8 (*Continued*)

Family and Species	Moore Park	Tooloom Plateau	Wian-garie	Mt. Pikapene	Bruxner Park	Moonpar
Rutaceae						
Bosistoa euodiformis					+	
Zieria sp.						+
Evodia micrococca		+		+		+
Zanthoxylum brachyacanthum		+	+	+		
Geijera salicifolia		+				
Melicope australasica			+			
Acronychia laevis	+					
A. baueri		+	+	+		
A. suberosa			+			+
Halfordia kendack			+			
Guilfoylia monostylis	+		+			
Meliaceae						
Cedrela toona var. *australis*	+	+	+			
Melia dubia	+			+		
Dysoxylum fraseranum		+	+	+		
D. rufum	+		+			
Pseudocarapa nitidula		+	+	+		
Synoum glandulosum					+	+
Flindersia australis		+	+	+		
F. schottiana				+		
F. xanthoxyla	+			+		
Euphorbiaceae						
Breynia oblongifolia		+		+	+	+
Hemicyclia australasica				+		
Bridelia exaltata				+		
Cleistanthus cunninghamii				+		
Croton insularis				+		
C. verreauxii		+		+	+	
Claoxylon australe			+	+	+	+
Mallotus philippinensis	+			+		
Alchornea ilicifolia				+		
Longetia swainii					+	+
Baloghia lucida	+	+	+	+		
Exoecaria dallachyana				+		
Homolanthus populifolius		+	+			+
Anacardiaceae						
Rhodosphaera rhodanthema	+					
Euroschinus falcatus			+	+		
Celastraceae						
Celastrus spp.		+		+		
Denhamia pittosporoides						+
Elaeodendron australe				+		
Siphonodon australe			+	+		
Icacinaceae						
Pennantia cunninghamii			+			
Citronella moorei		+				

TABLE 8 (*Continued*)

Family and Species	Moore Park	Tooloom Plateau	Wiangarie	Mt. Pikapene	Bruxner Park	Moonpar
Sapindaceae						
Diploglottis australis		+	+		+	+
Guioa semiglauca		+	+			+
Cupaniopsis anacardioides var. *parviflora*				+		
C. sp.			+	+		
Alectryon subcinereus	+			+		
A. tomentosus	+			+		
A. sp.				+		
Sarcopteryx stipitata		+	+		+	+
Jagera pseudorhus				+	+	
Elattostachys xylocarpa				+		
E. nervosa			+			
Arytera divaricata		+		+		
Mischocarpus pyriformis					+	
Harpullia hillii		+				
Akaniaceae						
Akania lucens			+		+	
Rhamnaceae						
Alphitonia petriei		+	+	+		
Vitaceae						
Vitis antarctica	+	+				+
V. hypoglauca						+
V. clematidea		+	+			
Elaeocarpaceae						
Sloanea australis		+	+		+	
S. woollsii			+		+	+
Elaeocarpus reticulatus					+	+
E. obovatus	+					
E. kirtonii			+			
Malvaceae						
Hibiscus heterophyllus				+		
Abutilon spp.	+					
Sterculiaceae						
Brachychiton discolor				+		
B. acerifolius			+		+	+
Argyrodendron trifoliolatum			+		+	
A. actinophyllum		+	+	+	+	
Flacourtiaceae						
Casearia multinervosa				+		
Thymeliaceae						
Wickstroemia indica		+				
Myrtaceae						
Tristania conferta					+	+
T. laurina					+	+
Backhouseia myrtifolia					+	
Myrtus acmenioides				+	+	
M. hillii				+		

TABLE 8 (*Continued*)

Family and Species	Moore Park	Tooloom Plateau	Wian-garie	Mt. Pikapene	Bruxner Park	Moonpar
Myrtaceae (*continued*)						
M. beckleri						+
Rhodamnia trinervia					+	+
R. argentea	+		+			+
Eugenia hemilampra			+			+
E. francisii				+		
E. corynantha					+	
E. brachyandra		+	+			
E. australis	+					
E. crebrinervis		+	+		+	
E. cyanocarpa			+		+	
Araliaceae						
Polyscias murrayi					+	+
P. elegans	+		+	+	+	
P. sambucifolius						+
Epacridaceae						
Trochocarpa laurina					+	+
Myrsinaceae						
Rapanea variabilis		+	+			+
Embelia australiana		+	+		+	+
Sapotaceae						
Niemeyera prunifera					+	
Planchonella australis		+	+		+	
P. myrsinoides				+		
Ebenaceae						
Diospyros australis		+				
D. pentamera		+	+	+	+	
Oleaceae						
Olea paniculata	+					
Apocynaceae						
Chilocarpus australis		+	+		+	
Alyxia ruscifolia				+		
Tabernaemontana orientalis					+	
Alstonia constricta				+		
Parsonsia sp.	+	+	+	+		+
Asclepiadaceae						
Hoya australis				+		
Boraginaceae						
Ehretia acuminata	+	+		+		
Verbenaceae						
Spartothamnus junceus				+		
Clerodendron tomentosum			+	+		
Gmelina leichhardtii					+	
Solanaceae						
Solanum auriculatum	+					
Duboisia myoporoides						+
Bignoniaceae						
Tecoma sp.	+	+	+	+		

TABLE 8 (*Continued*)

Family and Species	Moore Park	Tooloom Plateau	Wian-garie	Mt. Pikapene	Bruxner Park	Moonpar
Rubiaceae						
Randia benthamiana			+		+	+
Psychotria loniceroides						+
P. daphnoides			+			
Caprifoliaceae						
Sambucus sp.			+			
Compositae						
Helichrysum diosmifolium						+

Appendix II

ASH ANALYSIS

The sign (×) in Table 9 indicates that the sample so designated has been obtained from a locality not discussed in the present paper. A list of these localities is as follows:

Berowra: depauperate *Ceratopetalum* rain-forest in sandstone gully near Sydney.

Bilgola: a very much dwarfed headland rain-forest near Sydney, related to the *Cupaniopsis* alliance.

Bola Creek: gully rain-forest near Sydney belonging to the *Ceratopetalum–Diploglottis* association.

Bulli: a coastal example of the *Ceratopetalum–Diploglottis* association south of Sydney.

Cockrow: *Nothofagus*-dominated rain-forest near the Barrington Tops.

Gosford: gully rain-forest near Sydney, belonging to the *Ceratopatalum–Diploglottis* association.

Robertson: *Ceratopetalum–Diploglottis* association south of Sydney.

St. Ives: *Eucalyptus pillularis–E. saligna* wet sclerophyll forest on shale near Sydney.

Table 9

ASH ANALYSIS RESULTS

Percentage of oven-dry weight of leaf material

Species and Location	Ash	Ca	Na	K	PO_4
Brachychiton acerifolius					
Lamington Nat. Park—basalt	7·93	1·42	0·048	1·34	0·432
Bulli (×)	10·42	0·96	0·125	2·67	0·880
Wiangarie S.F.	9·30	0·52	0·056	3·05	0·811
Breynia oblongifolia					
St. Ives (×)	7·20	0·77	0·159	1·47	0·384
Bilgola (×)	5·92	0·63	0·302	1·22	0·183
Tooloom Plateau	14·03				
Mt. Pikapene	16·12				
Pine Creek—beach sands	8·98				
Casuarina torulosa					
St. Ives	3·18	0·34	0·130	0·36	0·126
Whian Whian	3·74	0·22	0·348	0·49	
Mt. Pikapene—tall woodland	3·83	0·13	0·157	0·40	
Barcoongere—good quality *Pinus*	4·21	0·12	0·408	0·47	
Cedrela toona var. *australis*					
Wiangarie S.F.	5·12	0·51	0·056	1·31	0·455
Koreelah	10·63	2·10	0·043	1·01	0·710
Ceratopetalum apetalum					
Lamington Nat. Park	7·86	0·59	0·047	0·45	0·108
Bulli	5·86	0·46	0·040	0·64	0·270
Berowra (×)	8·07	0·54	0·024	0·54	0·118
Bola Creek (×)	7·74	0·81	0·039	0·53	0·197
Whian Whian	6·06	0·24	0·067	0·63	0·146
Whian Whian	8·66	0·48	0·053	0·36	0·102
Dome Mountain—tree top	5·02	0·36	0·041	0·78	0·223
Dome Mountain—tree base	4·37	0·31	0·039	0·53	0·121
Claoxylon australe					
Gosford (×)	18·20	3·52	0·200	3·75	0·346
Wiangarie S.F.	15·43	2·87	0·154	2·95	0·593
Mt. Pikapene S.F.	14·75	2·99	0·118	1·83	0·488
Moonpar S.F.	14·02	2·69	0·070	2·31	0·376

TABLE 9 (*Continued*)

Species and Location	Ash	Ca	Na	K	PO_4
Cryptocarya glaucescens					
Gosford—inside rain-forest	3·87	0·62	0·124	0·64	0·207
Gosford—rain-forest margin	5·67	0·75	0·136	1·49	0·201
Diploglottis cunninghamii					
Bola Creek	9·00	0·80	0·288	1·18	0·471
Robertson (×)	5·94	0·62	0·083	0·89	0·500
Lamington Nat. Park—basalt	4·53	0·33	0·045	1·13	0·415
Gosford	9·87	1·12	0·128	0·77	0·369
Clouds Creek—basalt	10·98	1·78	0·110	0·98	0·376
Moonpar S.F.	6·34	0·66	0·139	0·42	0·254
Doryphora sassafras					
Lamington Nat. Park—basalt	3·06	0·50	0·037	0·42	0·190
Whian Whian—coachwood rain-forest	6·01	0·99	0·042	0·57	0·312
Robertson	5·72	0·76	0·052	1·07	0·311
Bulli	7·52	1·31	0·090	0·72	0·394
Bola Creek	7·51	1·01	0·098	1·42	0·323
Dome Mountain	4·33	0·65	0·065	0·70	0·198
Wiangarie S.F.	5·22	0·70	0·177	0·74	0·267
Cockrow (×)	5·71	0·85	0·046	0·93	0·305
Mt. Lindsay	5·24	0·83	0·147	0·82	0·257
Eucalyptus gummifera					
Barcoongere—good quality *Pinus*	3·40	0·23	0·344	0·52	0·183
Barcoongere—poor quality *Pinus*	3·09	0·23	0·232	0·65	0·121
Wiangarie S.F.—rain-forest margin	4·77	0·41	0·129	1·06	0·644
Eucalyptus planchoniana					
Barcoongere—poor quality *Pinus*	4·34	0·62	0·256	0·22	0·077
Eucalyptus saligna					
St. Ives	5·61	0·53	0·264	1·08	0·419
Tooloom Plateau—rain-forest margin	3·41	0·17	0·075	0·78	0·539
Cloud's Creek—basalt plain	4·92	0·66	0·226	0·67	0·458
Cloud's Creek—shale	4·76	0·48	0·176	0·76	0·380
Eugenia smithii					
Bulli	4·10	0·26	0·225	0·83	0·998
Robertson	3·62	0·44	0·163	0·41	0·184
Bola Creek	5·68	0·51	0·284	0·77	0·401
Berowra	4·91	0·65	0·206	0·66	0·153
Bilgola	3·77	0·34	0·181	0·53	0·262
Pine Creek—beach sand	5·42	0·72	0·108	0·43	0·798
Pine Creek—gully	3·48	0·37	0·139	0·49	0·302
Homolanthus populifolius					
Bilgola	6·10	0·29	0·287	0·72	0·324
Whian Whian—basalt	7·09	0·43	0·050	2·58	0·940
Whian Whian—obsidian	7·25	0·71	0·044	1·03	0·354
Orara West S.F.	5·62	0·69	0·056	1·06	0·459
Litsea dealbata					
Lamington Nat. Park—basalt	4·47	0·09	0·031	1·31	0·067
Whian Whian—basalt	4·39	0·05	0·026	0·44	0·020

TABLE 9 (*Continued*)

Species and Location	Ash	Ca	Na	K	PO_4
Litsea dealbata (*continued*)					
Whian Whian—acid rocks	3·30	0·46	0·043	0·42	0·213
Gosford	5·61	0·07	0·056	1·72	0·070
Tooloom Plateau	3·26	0·30	0·049	0·70	0·258
Brooklana	3·95	0·22	0·028	1·18	0·252
Nothofagus moorei					
Lamington Nat. Park	3·01	0·12	0·045	0·95	0·292
Brooklana	2·60	0·13	0·096	0·57	0·188
Dome Mountain	3·91	0·53	0·145	0·68	0·177
Cockrow	3·37	0·28	0·024	0·69	0·390
Orites excelsa					
Lamington Nat. Park—basalt	5·20	0·08	0·114	0·54	0·128
Whian Whian—acid rocks	4·86	0·18	0·083	0·30	0·120
Whian Whian—basalt	6·20	0·06	0·180	0·34	0·136
Dome Mountain	5·25	0·04	0·053	0·37	0·132
Cockrow	6·52	0·15	0·033	0·43	0·164
Pinus elliottii					
Clouds Creek—basalt plain	2·92	0·27	0·020	0·48	0·416
Brooklana	3·33	0·55	0·113	0·19	0·181
Barcoongere—good growth	3·68	0·58	0·026	0·23	0·219
Barcoongere—poor growth	2·33	0·33	0·033	0·24	0·112
Pittosporum undulatum					
St. Ives	8·01	0·74	0·072	2·36	0·278
Lamington Nat. Park—basalt	8·29	1·77	0·166	1·61	0·212
Dome Mountain—wet sclerophyll forest	6·92	0·43	0·097	2·39	0·177
Tooloom Plateau	10·36	1·75	0·145	2·58	0·255
Rhodamnia trinervia					
Gosford—inside rain-forest	5·33	0·68	0·053	0·34	0·214
Gosford—rain-forest margin	4·31	0·49	0·069	0·54	0·256
Whian Whian—basalt	5·38	0·31	0·064	0·69	0·545
Moonpar S.F.	4·65	0·35	0·074	0·76	0·226
Pine Creek—beach sand	6·57	0·28	0·039	0·54	0·898
Sloanea australis					
Lamington Nat. Park—basalt	4·15	0·66	0·099	0·72	0·240
Lamington Nat. Park—acid rocks	4·12	0·68	0·047	0·74	0·160
Whian Whian—basalt	6·11	1·20	0·098	0·66	0·251
Gosford	4·67	0·51	0·061	0·98	0·220
Bulli	5·40	0·79	0·102	1·15	0·387
Wiangarie S.F.	8·30	1·78	0·100	0·77	0·242
Smilax australis					
Gosford—rain-forest margin	5·51	0·83	0·099	1·08	0·152
Gosford—inside rain-forest	5·38	0·51	0·102	1·43	0·330
Whian Whian—acid rocks	6·59	0·63	0·138	2·21	0·190
Whian Whian—obsidian	5·47	0·94	0·109	0·97	0·287
Whian Whian—wet sclerophyll forest above basalt	5·33	0·88	0·149	1·06	0·298
Whian Whian—basalt	6·11	1·03	0·153	1·04	0·325

TABLE 9 (*Continued*)

Species and Location	Ash	Ca	Na	K	PO_4
Trochocarpa laurina					
Gosford—inside rain-forest	3·95	0·82	0·122	0·26	0·126
Gosford—rain-forest margin	3·64	0·65	0·087	0·65	0·127
Moonpar S.F.—wet sclerophyll forest	7·12	0·72	0·064	0·56	0·159
Moonpar S.F.—rain-forest	4·08	0·68	0·127	0·51	0·113
Wilkiea huegeliana					
Whian Whian—acid rocks	8·74	0·27	0·236	0·69	0·177
Whian Whian—basalt	10·76	1·19	0·242	0·47	0·183
Coffs Harbour—headland	11·18	1·03	1·55	1·00	0·473
Eugenia spp.—all from Wiangarie S.F.					
E. crebrinervis	6·46	0·78	0·265	0·89	0·307
E. brachyandra	3·76	0·05	0·034	1·39	0·632
E. hemilampra	3·62	0·30	0·181	0·52	0·212

INDEX